PHOCID PHYLOGENY AND DISPERSAL

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(With 9 figures and 1 table)

ABSTRACT

An attempt at a cladistic phylogeny of the Phocidae is presented. *Potamotherium* and *Semantor* are regarded as representatives of the sister group of the Phocidae, i.e. the Semantoridae (= Semantorinae of Tedford 1976). The Phocidae are divided into Phocinae and Monachinae and both subfamilies are subdivided into tribes, with every suprageneric taxon defined by synapomorphies. Poorly known fossil phocines and most of the Paratethyan seals are not taken into account, while some badly defined monachines are regarded as *incertae sedis*. This phylogeny, which envisages tribal divisions, allows for new hypotheses about the original homelands and southward migrations of the monachines. The Monachinae most probably originated in Europe and the three tribes of the subfamily crossed the Atlantic Ocean by way of the equatorial currents. One crossing is supposed for the Lobodontini and the Miroungini, while two east to west crossings seem to characterize the Monachini. It is also suggested that the southward migration of the Monachinae followed the Atlantic coasts of Africa and South America, and the Pacific coast of South America.

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INTRODUCTION

The problem of the pinniped relationships to other carnivores has been abundantly discussed by various authors (e.g. Mivart 1885; Scheffer 1958; McLaren 1960b; King 1964; Mitchell 1967; Mitchell & Tedford 1973; Sarich 1969a, 1969b, 1975). Tedford (1976) summarized the data of this problem and reached the conclusion that the group is biphyletic. The pinnipeds (phocid and otarioid seals) are included by Tedford in the infraorder Arctoidea. Within this group the otarioid seals are more closely related to the parvorder Ursida and the phocid seals to the parvorder Mustelida. The purpose of this paper is to analyse the relationships within the Phocidae as defined by Tedford (1976) (= Phocidae s.1.). The problem of relationships of the phocids to the genera *Potamotherium* and *Semantor* and to the lutrines, although frequently considered by previous writers, will be briefly discussed; the relationships of these musteloids to the other carnivores will not be considered here, having been clearly outlined by Tedford (1976).

PHOCID PHYLOGENY

RELATIONSHIP OF PHOCIDS TO THE OTHER MUSTELOIDEA

The study of Mivart (1885) represents the first record in the literature of a discussion on phocid–lutrine relationship. In this work *Potamotherium* was definitely considered to be a lutrine, which has been the opinion of most authors since that time. In his study Mivart exposed several features that closely relate seals to otters and otariids to bears, thus demonstrating for the first time the polyphyletism of the pinnipeds. This idea is now almost universally accepted among palaeontologists. The features outlined by Mivart (1885: 498) mostly concern the skull (orbitary and auditory region), the mandible, and the femur.

Potamotherium valetoni (Lower Miocene of France) is so lutrine-like that it was for a long time considered to be a very specialized otter. It is regarded as such by Kellogg (1922) who ratifies Mivart's arguments about lutrine–phocid similarities and notes several characters of *Potamotherium* that '. . . may indicate relationships with the Phocidae', and concludes that '. . . one of the forbears of *Potamotherium* was the source and that the Lutrinae and the Phocidae are both descendants of that type' (Kellogg 1922: 86). This definitely anticipates the interpretation given here (Fig. 1).

The striking similarities of *Potamotherium* and the Phocidae have been noted elsewhere. Some authors consider the resemblance to be of phylogenetical significance (Kirpichnikov 1955; McLaren 1960b; Mitchell & Tedford 1973; Tedford 1976), while others believe *Potamotherium* to be related to lutrines, the phocid-like features of this aquatic carnivore being due to convergence (among others, Thenius 1949a, 1949b, 1969; Viret 1955, Piveteau 1961).
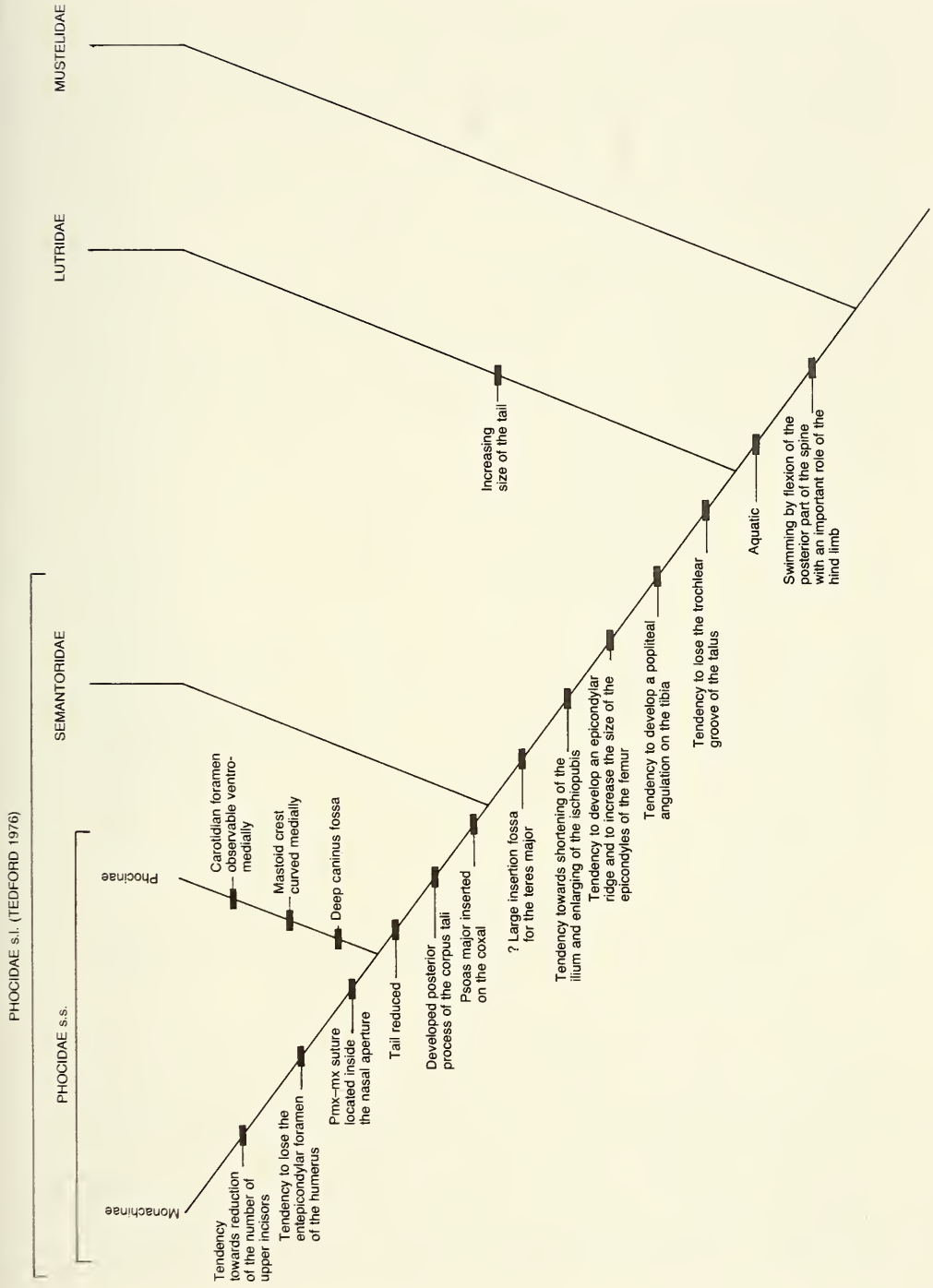
Fig. 1. Assumed relationships of the Musteloidea.

PHOCIDAE s.l. (TEDFORD 1976)

PHOCIDAE s.s.

MUSTELIDAE

LUTRIDAE

SEMANTORIDAE

Phocinae

Monachinae

Tendency towards reduction of the number of upper incisors

Tendency to lose the entepicondylar foramen of the humerus

Prmx-mx suture located inside the nasal aperture

Tail reduced

Carotidian foramen observable ventro-medially

Mastoid crest curved medially

Deep caninus fossa

Developed posterior process of the corpus tali

Psoas major inserted on the coxal

? Large insertion fossa for the teres major

Tendency towards shortening of the ilium and enlarging of the ischiopubis

Tendency to develop an epicondylar ridge and to increase the size of the epicondyles of the femur

Tendency to develop a popliteal angulation on the tibia

Tendency to lose the trochlear groove of the talus

Increasing size of the tail

Aquatic

Swimming by flexion of the posterior part of the spine with an important role of the hind limb

Another frequently discussed phocid-like aquatic carnivore is *Semantor macrurus* from the Upper Miocene of Pavlodar (Kazakstan). The phocid features of *Semantor macrurus* are so striking that they led Orlov (1933) to classify this form in a new family of Pinnipedia, the Semantoridae. Thenius (1949*b*) regards the similarities between *Semantor* and phocids to be not as numerous or as important as stated by Orlov, and he supports Friant (1947) in ascribing them to convergence. However, many authors (Kirpichnikov 1955; McLaren 1960*b*; Mitchell & Tedford 1973; Tedford 1976) have also argued that these similarities are of phylogenetical significance.

Tedford (1976), in a cladistic analysis of the pinniped relationships, relates the Semantoridae (in which he includes the genera *Potamotherium* and *Semantor*) to the Phocidae, both being the sister group of the Mustelidae. Tedford's classification introduces a slight ambiguity because the Phocidae (*sensu stricto = sensu* Simpson 1945 and Romer 1966) and the Semantoridae are considered to be subfamilies. The Phocidae (*sensu lato = sensu* Tedford 1976) include the Phocinae (*s.l.*), which correspond to the Phocidae (*s.s. = sensu* Simpson 1945), and the Semantorinae (*sensu* Tedford 1976). The taxon Phocidae now has two interpretations: *s.l.* (*= sensu* Tedford 1976) and *s.s.* (*= sensu* Simpson 1945). Although Tedford's classification is logical in a strictly cladistic sense, both groups are, for the sake of convenience, here regarded as families. Moreover, according to the interpretation of the relationships of the four groups given here, Phocidae, Semantoridae, Lutrinae and other Mustelidae (Fig. 1), the Lutrinae will be given family rank (i.e. Lutridae). This is an application of the sequence process as defined by Nelson (1974). The four families are grouped into the Musteloidea. Be that as it may, these terminological points are considered to be of little significance here since the present study focuses on the relationships of the groups cited above rather than their classification.

Tedford (1976) has pointed out three characteristics that could define the Semantoridae and the Phocidae:

(i) swimming mainly by flexion of the trunk,
(ii) dentition reduced to homeodonty,
(iii) an enlarged process for the teres major muscle, which occupies the lateral border of this process.

These three features cannot all be regarded as synapomorphies. Among the carnivores, swimming mainly by flexion of the trunk is found not only in phocids but also in otters and this characteristic is, therefore, inappropriate as a synapomorphy of Phocidae and Semantoridae. Homeodonty is also found among carnivores in the Otariidae and represents a general tendency in all toothed marine mammals. Furthermore, *Potamotherium* does not, in fact, have a homeodont dentition, and that of *Semantor* is unknown. Therefore, this characteristic is also an inadequate synapomorphy for the Phocidae and the Semantoridae. The enlarged insertion for the teres major muscle of the phocids

and *Potamotherium* is absent from all other carnivores, as clearly demonstrated by Tedford (1976), and the teres process of these musteloids is very different from the one observed in ursids and procyonids. Although the scapula of *Semantor* is unknown, the enlarged insertion for the teres major muscle is hypothetically regarded as a synapomorphy of phocid (*s.s.*) and semantorids.

The pelvis of the phocids (*s.s.*) is very typical and distinct from those of other carnivores. The ilium is very short, wide, triangular shaped and extroverted, while the ischiopubis is very enlarged. Considering the coxal of *Potamotherium*, Savage (1957: 215) has already stated that it 'more resembles *Phoca* than *Lutra*'. In fact, the short outwardly flexed ilium, the weak symphysis, and the long and dorsally elevated ischium enclosing a large obturator foramen are definitely phocid-like and show in *Potamotherium* an obvious tendency towards the phocid coxal condition. The coxal of *Semantor* is so phocid-like that, if founded isolated, it would almost certainly be identified as a primitive phocid. The ilium is even shorter and more extroverted than in *Potamotherium*, and approaches more a primitive phocid condition than a lutrid one. The enlargement of the ischiopubis, even longer than in some Monachinae, and the pubic symphysis orientated downward are also typically phocid-like. The coxal in otters is very different from that in Semantoridae. In otters the ilium is always very long and the ischiopubis short (this condition is especially well marked in the sea otter). In all otters, as in all terrestrial carnivores, the ilium is longer than the ischiopubis or approximately of the same size (see Taylor 1914, figs 10–12). In the Semantoridae and obviously in the Phocidae, the ilium is always much shorter than the ischiopubis. These conditions have been noted on all the coxae of semantorids and lutrids examined during this study.

The femora of semantorids and phocids differ radically (as stated below), the former having a second trochanter while it is always absent in the latter. In this respect the similarity existing between the non-phocid carnivores (including the semantorids) is regarded here as a symplesiomorphy. Nevertheless, the femora of phocids and semantorids show a common apomorphic tendency to develop an epicondylar ridge on the medial side of the distal extremity. This tends to give an oblique position to the condylar surface of the distal extremity of the femur relative to the axis of the bone [already observed by Savage (1957) in *Potamotherium*]. In otters (including sea otters) the epicondylar ridge is totally absent and, contrary to the phocid condition, this region of the femur is somewhat concave; moreover, in otters the condylar surface is perpendicular to the shaft of the bone. The tendency to develop an epicondylar ridge on the semantorid femur bears resemblance to the S-shape of the medial border of the phocid femur; in otters this border is C-shaped (in anterior view). These conditions are related to the fact that the condyles of the femur seem to have moved laterally and distally in the phocids and the semantorids, while the movement is medial and proximal in otters (this is especially clear in the sea otter, *Enhydra lutris*).

Another similarity between the femora of phocids and semantorids is the tendency for the size of the epicondyles to be strongly developed, while in all otters the epicondyles are very little developed. As with the development of the epicondylar ridge, this condition is related to an important use of the flexor and extensor muscles of the foot (peroneus longus, extensor digitorum longus, gastrocnemius caput laterale and caput mediale, flexor digitorum superficialis). This clearly indicates that, as in the phocids, the movements of the foot were essential in semantorid swimming. In the otters, the action of the foot is not as important and the propulsive movement of the hind limb is a powerful backward extension of the whole limb (see below), being, therefore, a more generalized movement.

These two similarities between the femora of phocids and semantorids, i.e. a tendency to develop an epicondylar ridge and to increase the size of the epicondyles on the femur, are synapomorphic trends of the group.

As in the phocids, but to a lesser degree, *Potamotherium* and *Semantor* show a tendency towards a shorter femur; in this respect these two genera are closer to the phocids than to the lutrids.

The tibia of *Semantor* is typically phocid-like and the same could be said of this bone as of the coxal—if found isolated it would have been classified as belonging to a primitive phocid. It definitely differs from the lutrid tibia in having its medial border very convex in its proximal third. This well-marked convexity, where the popliteus is inserted, gives the tibiae of phocids and *Semantor* an S-shape that is never seen in any otter. In this group the medial side of the tibia is, on the contrary, deeply concave. The condition observed in *Potamotherium*, although less marked than in *Semantor*, is similar and its tibia resembles more closely that of *Semantor* than that of *Lutra* or *Enhydra*.

Although McLaren (1960b) stated that the tibia and fibula of *Semantor* were fused proximally as in the phocids, Orlov (1933: 196) in his description definitely noted proximally articulated bones.

As stated by McLaren (1960b), the talus of *Semantor*, as in phocids, has lost the groove of the trochlea, which is usually well marked in the terrestrial carnivores. Savage (1957) stated that the groove of the trochlea of *Potamotherium* talus is shallower than in the lutrids, therefore approaching the phocid and semantorid condition. However, both tali of *Semantor* and *Potamotherium* are lacking the posterior process that is a typically phocid condition.

In the foot of *Potamotherium miocenicum* the MtV is so phocid-like that one specimen from the Tortonian deposits of Neudorf (ČSR) (Thenius 1950) was at first referred by Toth (1944) to *Miophoca vetusta*. This misunderstanding is indicative of the great similarity that exists between *Potamotherium* and the Phocidae.

It is also worth noting that *Potamotherium* and *Semantor* have a long tail, a character that seems to relate them to the lutrids (Thenius 1949b). However, the tail of these musteloids is much shorter even than the short tail of the sea otter (*Enhydra lutris*) which could approach that of a primitive terrestrial

musteloid in size. The wing-like transverse process of the first three caudal vertebrae of *Potamotherium* and *Semantor* is much less developed than in lutrids and indicates less use of the tail in swimming. As indicated by Savage (1957: 191), in aquatic mammals, where the primary organs of propulsion are usually situated posteriorly, the tail and hind limbs develop in inverse proportions. In *Potamotherium* and *Semantor* the little developed tail (compared to otters) is in accord with an important use of the hind limb in swimming. As a matter of fact, the anatomy of the semantorid hind limb indicates that it was used in swimming, probably in a different way from that of the otters, but more similar to that of the phocids. The swimming action of the hind limbs of otters is an alternating or simultaneous paddling (Fischer 1939, and personal observations). This movement is made anteroposteriorly and the plane of the foot is always approximately perpendicular to the sagittal plane of the animal. The action of the limb is simply a full backward extension. When seals swim the paddling of the hind limbs is always alternating, lateromedial, and the plane of the foot is always parallel to the sagittal plane. One of the actions of the limb is an adduction of the leg. In such swimming the feet are always posterior to the pelvis. The adduction of the leg is facilitated by the enlarged ischiopubis and by the torsion of the tibia and of the distal extremity of the femur, two conditions that tend to place the tibia in front of the ischiopubis (the limb being orientated backward). Such a position increases the lever arm of the adduction of the leg and reinforces the action of the adductor muscles (semimembranosus, semitendinosus, gracilis, and biceps femoris). The anatomy of the hind limbs of the semantorids (mentioned above) clearly indicates a phocid-like use of these limbs in swimming, which is a condition that separates the phocids and semantorids from the lutrids. The conclusion of Helbing (1921) concerning swimming in *Potamotherium*, although not very clear, seems to indicate a lesser mobility of the femur and a more important role of the leg (tibia and fibula) and of the foot than in the lutrines. This definitely agrees with the interpretation given here. All the similarities of the semantorids to the lutrids have most probably to be considered as symplesiomorphies within the 'phocid–semantorid–lutrid' group. So too must be considered the fairly well-developed tail of the semantorids.

The Phocidae, the Semantoridae and the Lutridae constitute a monophyletic group defined by the following synapomorphies:

 (i) aquatic Musteloidea,
 (ii) swimming by flexion of the posterior part of the spinal column, with the hind limbs playing an important role.

The lutrid synapomorphies are not examined in detail, this group being considered here only in its relation to the phocid–semantorid group. However, it is worth noting that the clear tendency to increase the size and the power of the tail could represent an important synapomorphy of the Lutridae.

The Semantoridae–Phocidae may be defined by at least five synapomorphies:

  (i) large insertion fossa for the teres major (?),
 (ii) shortening of the ilium and enlarging of the ischiopubis,
(iii) tendency to develop an epicondylar ridge and to increase the size of the epicondyles on the femur,
(iv) tendency to develop a popliteal angulation on the tibia,
 (v) reduction of the trochlear groove of the talus.

The definition of the semantorid synapomorphies is problematical because the anterior half of the skeleton of *Semantor* is largely unknown (one humerus was referred by Kirpichnikov (1955) to *Semantor*, and perhaps belongs to the holotype). Most of the synapomorphies of *Potamotherium* and *Semantor* are either synapomorphies of the phocid–semantorid group, or symplesiomorphies of the phocid–semantorid–lutrid group. Nevertheless, in view of the great similarities between *Potamotherium* and *Semantor*, it is here tentatively concluded that they belong to the same group. Moreover, *Potamotherium*, which comes from the European Lower and Middle Miocene, is temporally well situated to be on the lineage leading to *Semantor* from the Upper Miocene of western Siberia. This is corroborated by the fact that the features cited above are all more pronounced in *Semantor*. However, the presumed relationship of these two musteloids will have to be confirmed by the discovery of new material (in particular cranial material) of *Semantor*.

The present interpretation of the relationship of *Potamotherium* and *Semantor* to the other Musteloidea differs from that of Thenius (1949a, 1949b, 1969, 1972) who relates them to the lutrids rather than to the phocids, as is done in this paper. However, the opinion presented here is in agreement with Kirpichnikov (1955), McLaren (1960b), and Tedford (1976).

THE PHOCIDAE

The Phocidae (*s.s.*) are defined by three features, two of them are unique among the mammals. In non-phocids the psoas major distal insertion is located posteromedially on the second trochanter of the femur, while in the phocid it is inserted on the ventral edge of the ilium on the posteroventral ischiatic spine, just anterior to the iliopectineal eminence (Figs 2–3). This modification of the psoas major distal insertion represents an adaptation to aquatic life in the Phocidae (De Muizon 1981b). The swimming of true seals is achieved by alternating adductions of the hind limbs in conjunction with strong undulations of the posterior part of the spinal column. Both movements are almost always on a horizontal plane. The quadratus lumborum and the psoas minor (like the psoas major) both have their proximal insertion on the ventral side of the lumbar vertebrae, their distal insertion being on the ventral edge of the ilium; when contracted alternatively, they emphasize the lateral flexion of the spinal column. In the phocid swimming action, the insertion of the psoas major on the ventral edge of the ilium obviously reinforces the horizontal undulatory movements, while in terrestrial mammals the psoas major inserted on the femur acts as a flexor of the thigh, which assists the forward movement of the
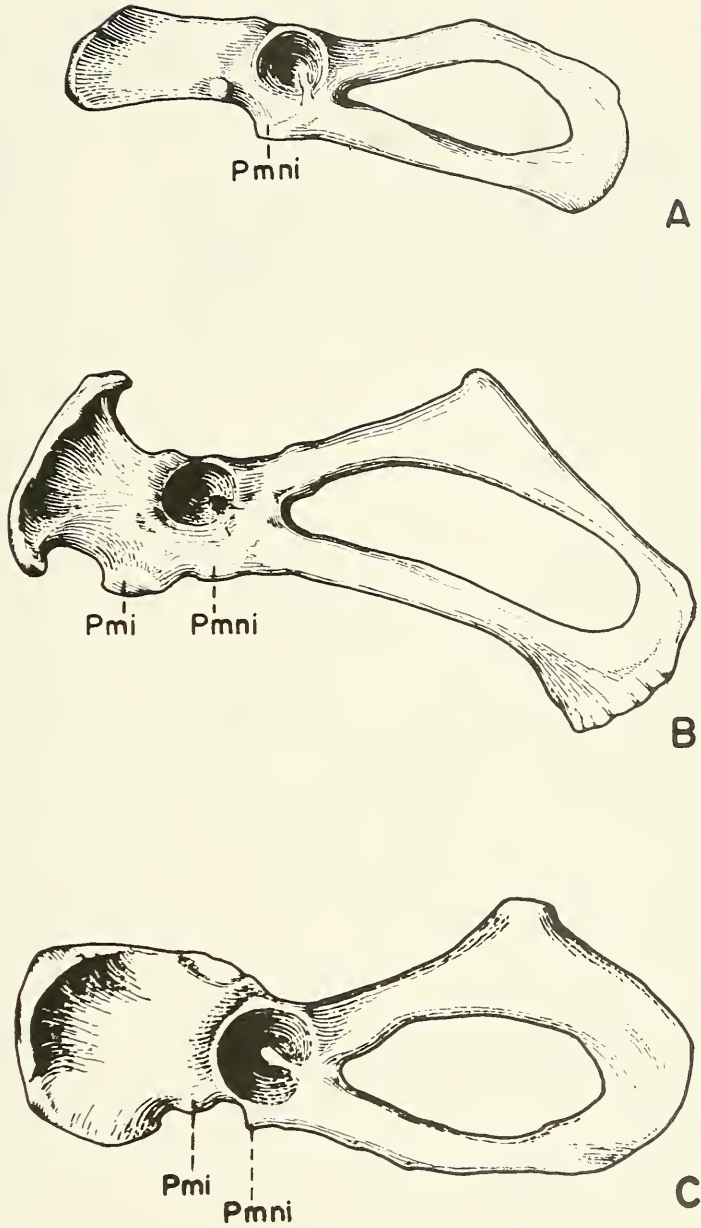
Fig. 2. Left innominates in lateral aspect. A. *Zalophus californianus* (from Howell 1929). B. *Pusa hispida* (from Howell 1929). C. *Monachus monachus* (from Ray 1976). Pmi—posteroventral ischiatic spine where the insertion of the psoas major is located (in the Phocidae); Pmni—iliopectineal eminence, where the insertion of the psoas minor is located.
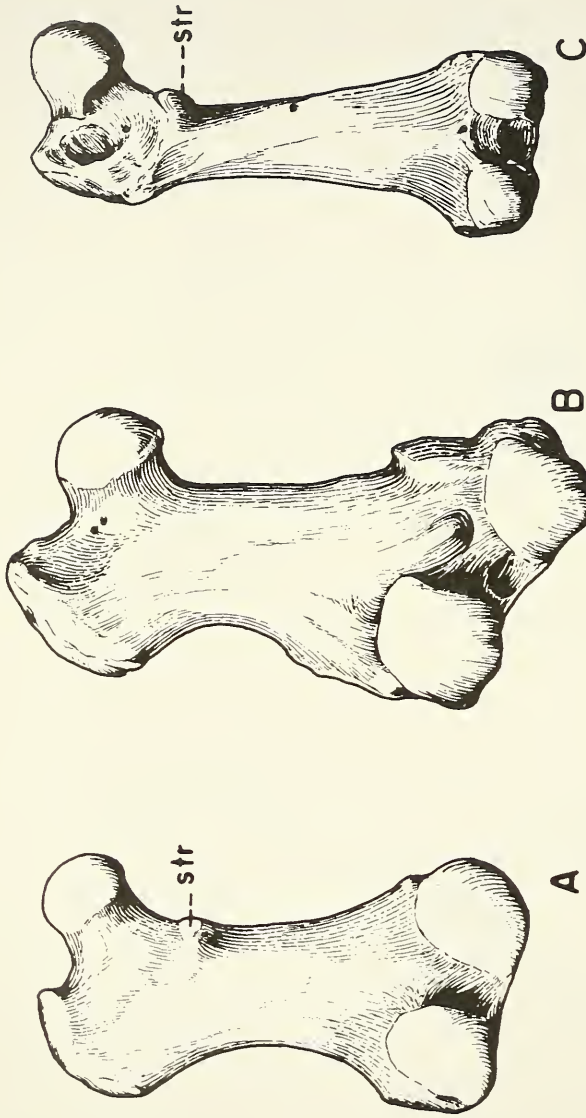
Fig. 3. Left femora in posterior aspect. A. *Zalophus californianus* (from Howell 1929). B. *Pusa hispida* (from Howell 1929) C. *Potamotherium valetoni* (approx. x 1, 2); str—second trochanter of the femur where the insertion of the psoas major is located.

hind limb in walking and running. The psoas major insertion on the ilium, a synapomorphy of the Phocidae *s.s.*, is not found in the Semantoridae where the second trochanter of the femur, absent in the Phocidae, is always present.

In other respects the talus of the Phocidae shows a very strong posterior process of the corpus tali, which has a groove on its plantar aspect indicating the passage of the flexor hallucis longus tendon. This condition is due to the very important action of the flexor hallucis longus in phocid swimming. During the adduction of the leg, which takes place in the alternating movement of the hind limb, this muscle prevents the flexion of the foot and the extension of the fingers; this causes resistance to the water current induced by this adduction of the leg and, as a result, creates the propulsion. At the end of the movement it reinforces its propulsive action by a powerful extension of the foot. This muscle is probably the most active in the ankle movement during the phocid swimming. The posterior process of the corpus tali considerably increases the leverage of the extension of the foot, and hence strengthens this movement which is essential to phocid swimming. In fact, the flexor hallucis longus of phocids is better developed than in any other mammals and, as noted by Howell (1929), its tendon is by far the strongest one of the foot. On land this characteristic, among others, prevents significant anterior flexion of the foot and explains why these animals always keep their feet as an extension of the body. The condition of the phocid talus is unique among mammals and is considered here as another synapomorphy of the family.

The Phocidae are also defined by an appreciable reduction of the tail, which, as with the two synapomorphies cited above, is correlated to the important action of the hind limbs in swimming.

The Phocidae (*s.s.*) are here divided into two subfamilies: the Phocinae *s.s.* and the Monachinae. The subfamily Cystophorinae Simpson, 1945, is no longer recognized as valid, its taxa having been assigned instead to the Phocinae and to the Monachinae (King 1966). Although some authors still regard the Cystophorinae as a monophyletic group (Thenius 1969, 1972), King's interpretation is followed here.

The Phocinae may be defined by three synapomorphies:

  (i) the mastoid crest is curved medially in such a way that it is possible to observe the mastoid in dorsal view of the skull. This condition is also found in the monachine *Ommatophoca* (as noted by Ray 1976*a*), but in this genus the crest is straight,

 (ii) the carotid foramen is visible ventromedially and not ventrally as in the Monachinae. This feature is not as constant as (i), but seems to represent a tendency in the group, and is the consequence of a very strong inflation of the tympanic bulla,

(iii) the development, on the lateral side of the maxillary, of a well-marked fossa for the insertion of the caninus muscle. This condition exists only in the Phocinae and seems to represent an apomorphy. However, *Mirounga*, a monachine, often shows a well-marked caninus fossa. In fact, in this

genus the strong development of the caninus seems to be related to the extreme size of the upper lip, modified into the probicis of the males, which generally have a deeper caninus fossa than females. The plesiomorphic condition seems to be a weak caninus that disappears in most Monachinae (it has not been observed by Piérard (1971) in *Leptonychotes weddelli*); it is strengthened in the Phocinae *s.s.* and by parallel evolution, in *Mirounga*.

The Monachinae are characterized by three synapomorphies:

(i) the premaxilla–maxilla suture is, in its medial part, located inside the nasal aperture (in *Homiphoca capensis* it is situated on the nasal aperture border). In lateral view the visible part of the premaxilla is, therefore, partially hidden by the maxilla. The plesiomorphic condition is observed in most of the Phocinae and all the other carnivores where the part of the premaxilla that is visible laterally is more or less of constant width and where the premaxilla–maxilla suture is always external to the nasal aperture (Fig. 4),

(ii) there is a tendency for a reduction of the number of upper incisors to four or two. However, *Monotherium? gaudini* from the Middle Miocene of the Abruzze (Italy) is a Monachinae and yet retains six upper incisors (a plesiomorphic condition),

(iii) there is a clear tendency for the entepicondylar foramen of the humerus to be lost; this condition is only a tendency because two genera of Monachinae (*Monotherium* and *Homiphoca*) have such a foramen. All the phocine seals have an entepicondylar foramen which represents a plesiomorphic condition.

There are other apomorphic tendencies in both subfamilies, mainly in the postcranial skeleton. For instance, in the monachines, excluding *Leptonychotes weddelli*, the deltopectoral crest reaches the distal extremity of the humerus shaft, while in the phocines it is abruptly interrupted midway along the shaft. The phocine condition seems to be apomorphic, but *Leptonychotes weddelli*, a monachine, shows a similar disposition. Moreover, the humerus of *Leptophoca lenis*, a primitive Middle Miocene phocine, shows a condition rather similar to that in *Potamotherium* and mustelids. The reduction of the epicondylar crest is most probably an apomorphic tendency of the monachines, but this feature can also be found by convergence in *Platyphoca vulgaris*, a Pliocene phocine. On the femur the lowering of the trochanter and the reduction of the trochanteric fossa are also apomorphic tendencies of the monachines, but most of the fossil and one living (*Lobodon carcinophagus*) representatives of this group have a well-marked trochanteric fossa. In other respects, the rotulian facet on the femur of the monachines shows a clear tendency to become compressed and more oval and the calcaneum to be more robust in this group than in the phocines (De Muizon 1981a, tables 8–13); these two features are also regarded here as apomorphic. However, these apomorphic tendencies, which are not
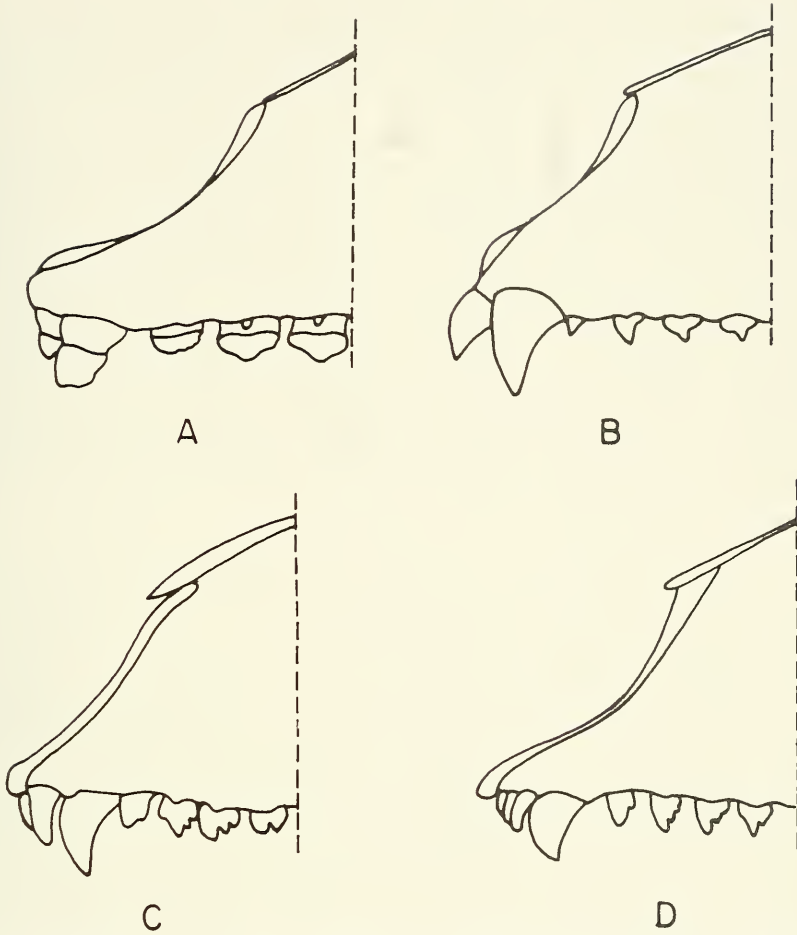
Fig. 4. Relationships of the nasal, maxilla and premaxilla in some Phocidae. A. *Monachus tropicalis*. B. *Leptonychotes weddelli*. C. *Phoca vitulina*. D. *Pagophilus groenlandicus*.

constant as the three used in Figure 1, were not included in the cladogram. Nevertheless, circumspectly they can be employed as diagnostic features of both subfamilies.

THE PHOCINAE *S.S.*

In view of the scarcity of cranial remains of fossil phocines, only the phylogeny of living representatives of this group will be considered.

One feature allows the separation of the subfamily into two tribes, Erigna- thini and Phocini. It is the gluteal fossa on the lateral side of the ilium that is extremely deep in the Phocini (King 1964; Hendey & Repenning 1972) but is shallow in the Erignathini and all the monachines. The condition of the Phocini

is an apomorphic feature related to the strengthening of hind limb musculature. No synapomorphy could be found for the Erignathini, a tribe represented at present by one species only (*Erignathus barbatus*). It is possible that the study of fossil phocines, none of which having a deep gluteal fossa, may require a redefinition of the Erignathini.

The Phocini are known by the living genera *Phoca*, *Pusa*, *Halichoerus*, *Cystophora*, *Pagophilus*, and *Histriophoca*. Burns & Fay (1970), in a numerical taxonomic analysis, regarded the genera *Phoca*, *Pusa*, *Histriophoca* and *Pagophilus* as subgenera of *Phoca*. This analysis did not consider either the character state (apomorphic or plesiomorphic) or the relative importance of the features taken into account, and McLaren (1975: 44) already stated the danger of such a method which '. . . may tend to obscure phyletic links'. In the present study some features assumed to be apomorphic were observed, and this prompted a division of the Phocini into two groups, namely, the '*Phoca–Pusa–Halichoerus*' group and the '*Cystophora–Histriophoca–Pagophilus*' group (Fig. 5).

Phoca–Pusa–Halichoerus

The three genera show a clear tendency toward closing of the external cochlear foramen by an excrescence of the tympanic bulla external to the tympanic cavity, and confers a better resistance to water pressure (see p. 193, Fig. 6). This is considered here as a synapomorphy of this group.

Halichoerus shows the obvious apomorphies of extreme height of the snout and of the nasal aperture, and a clear tendency towards single-rooted cheek teeth. Other phocids almost always have double-rooted cheek teeth.

The genera *Phoca* and *Pusa* are very similar and some authors (e.g. Chapskii 1955*a*; Burns & Fay 1970; Grigorescu 1976; Ray 1976*b*; Repenning *et al.* 1979) regard the latter as a subgenus of the former. They differ from *Halichoerus* by, among other characters, the more anterior palatine foraminae, the more reduced premaxillary foraminae, and the larger nasals. These three characteristics apparently represent apomorphic tendencies in the Phocinae as a whole and can be regarded as the synapomorphies of *Phoca* and *Pusa*. These two taxa could be referred either to genera (following Scheffer 1958; King 1964; Kirpichnikov 1964) or to subgenera (following Chapskii 1955*a*; McLaren 1960*a*; Burns & Fay 1970). However, this subjective difference is here regarded as being of little significance, and *Phoca* and *Pusa* are tentatively listed as sister genera. This relationship has already been suggested by various authors (McLaren 1960*a*; Kirpichnikov 1964; Chapskii 1955*a*; McLaren 1975).

Phoca pontica, referred by Grigorescu (1976) to the subgenus *Pusa*, almost certainly belongs to the *Phoca–Pusa* group. This conclusion has been accepted by various authors (Chapskii 1955*b*; McLaren 1960*a*, 1975; Kirpichnikov 1964; Repenning *et al.* 1979). According to Grigorescu, the auditory region of '*Phoca*' *pontica* is very close to that of *Pusa*, but as no specimen, cast, or adequate illustrations were available during this study, the characteristic struc-
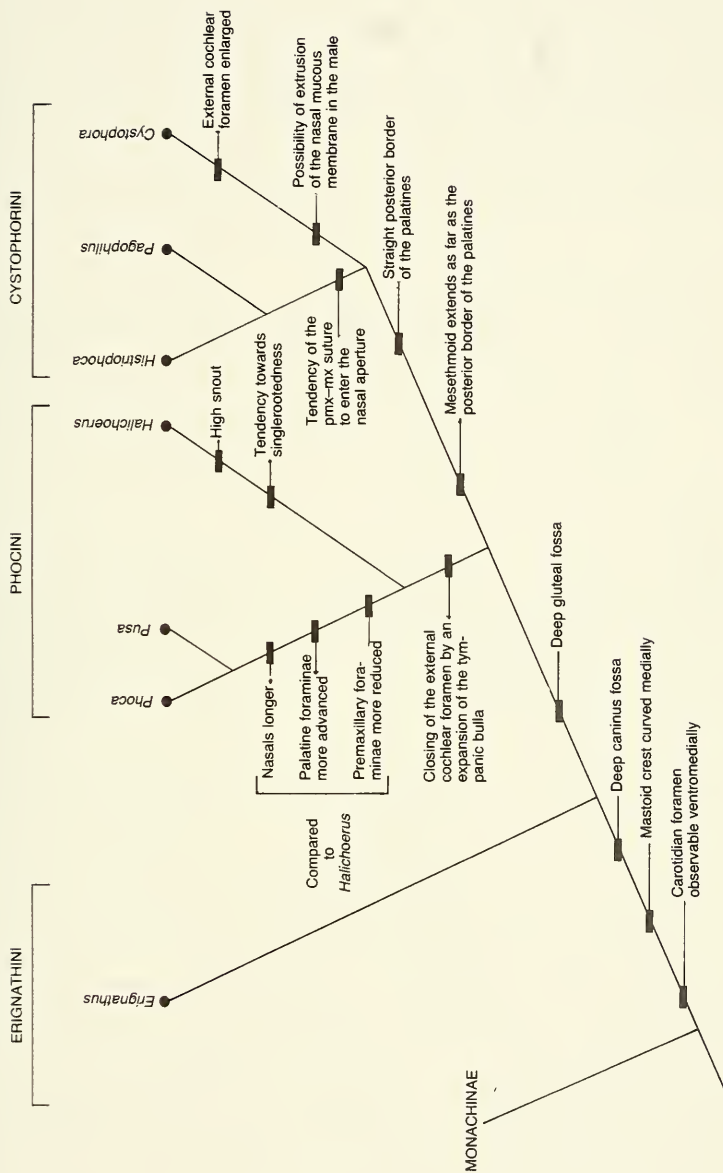
Fig. 5. Assumed relationships of the Phocinae.

ture of the auditory region of the *Phoca–Pusa–Halichoerus* group in '*Phoca*' *pontica* could not be confirmed. '*Phoca*' *vindoboniensis*, whose auditory region is unknown, was excluded from consideration. The only known specimen of '*Phoca*' *vindoboniensis* is the incomplete skeleton lacking the skull described by Toula (1898). Nevertheless, Grigorescu (1976) has expressed the opinion that it may probably be related to the *Phoca–Pusa* group and he concludes that '*Phoca*' *pontica* from the Bessarabian deposits (Middle Sarmatian) of the Black Sea and Caspian Basin is a descendant of '*Phoca*' *vindoboniensis* from the Volhynian deposits (Lower Sarmatian) of the Vienna Basin. Grigorescu's interpretation is highly probable but it has still to be confirmed by the discovery of complete skulls of both species.

Cystophora–Pagophilus–Histriophoca

In these three genera the posterior border of the palate is roughly straight or forms a very shallow double arch. This feature seems to be fairly constant for *Pagophilus* and *Cystophora*, but Burns & Fay (1970) observed it on only half of the skulls of *Histriophoca* that they have examined, the other half having a distinct notch. This notch, situated in the medial part of the posterior border of each palatine, is also common in *Phoca* and *Pusa* (Burns & Fay 1970), and during the present study it was observed in *Monachus*, *Leptonychotes*, and *Hydrurga*. If this notch were absent, the posterior border of the palate would be roughly straight in *Histriophoca* and fairly deeply arched in *Phoca* and *Pusa*. Apparently *Cystophora*, *Pagophilus* and *Histriophoca* have a tendency towards a straight posterior border of the palatine, although it is not as constant in *Histriophoca*. This feature is known among the phocids in these three genera only and for this reason it is interpreted as an apomorphic condition.

Also in these genera, the mesethmoid extends as far as the posterior border of the palatines, whereas in the other Phocidae it separates from the palatines at a point well anterior to it. This feature, which is very probably related to the preceding one, was observed by Burns & Fay (1970) in only half of their *Histriophoca* specimens, while it was constant in all the *Cystophora* and *Pagophilus* specimens examined in the present study. As with the preceding feature, the *Cystophora* group shows an obvious tendency for the mesethmoid to reach the posterior edge of the palate. This condition, which is not found in other Phocidae, seems to represent a synapomorphy of the group. No satisfactory functional interpretation of these two characteristics could be determined.

In contrast to other Phocinae, the three genera of the *Cystophora* group have a well-marked external cochlear foramen (Fig. 6). This is regarded here as a plesiomorphic condition among the phocids (see p. 195) and therefore it cannot be used to define the group. In *Histriophoca* the external cochlear foramen is located in a conspicuous pit at the limit of the petrosal and of the mastoid (Burns & Fay 1970). The arrangement is identical in *Pagophilus*, but in *Cystophora* the pit is modified into a groove that separates the mastoid and the

petrosal. This pit or groove is absent in the other phocines, but the condition observed in the three genera of the *Cystophora* group is very similar to that of *Monachus* (subfamily Monachinae) and it is regarded as a symplesiomorphy among the Phocidae (see p. 195).

The resemblances between *Histriophoca* and *Pagophilus* are striking but could represent symplesiomorphies. However, these two genera share an apomorphic feature: the maxilla–premaxilla suture (in the lateral view of the skull) tends to be located on the crest of the lateral edge of the nasal aperture (sometimes slightly inside) (Fig. 4). This feature is a synapomorphy found in the Monachinae (see p. 193), which is paralleled in *Histriophoca* and *Pagophilus*. As with *Phoca* and *Pusa*, *Histriophoca* and *Pagophilus* are here regarded as valid genera.

The obvious specializations in *Cystophora* are:

(i) in the adult male the nasal mucous membrane can be extruded to form a red 'bladder' sometimes as big as the head,

(ii) the posterior extremity of the ascending ramus of the premaxilla is very low and always at least 2 to 3 cm from the nasal,

(iii) the upper incisors are reduced to four and the lower to two, in contrast to other phocines that have six upper and four lower incisors.

Discussion

The preceding cladistic analysis of phocines contrasts in some respects with the relationships suggested by Burns & Fay (1970). They regard *Phoca*, *Pusa*, *Histriophoca*, and *Pagophilus* as subgenera of *Phoca*, thus including the four taxa in the same group. The interpretation of Burns & Fay is in agreement with Doutt (1942) who referred the four genera to *Phoca* but without any subgeneric division. According to the interpretation presented here, the genus *Phoca* (*sensu* Burns & Fay 1970 and Doutt 1942) is polyphyletic, since *Phoca* is clearly related here to *Pusa*, while *Pagophilus* is related to *Histriophoca*. Nevertheless, if subgenera are to be recognized, then *Phoca* Linnaeus, 1758, has priority over *Pusa* Scopoli, 1777, in the first group, and in the second group *Pagophilus* Gray, 1844, has priority over *Histriophoca* Gill, 1873. *Pusa* and *Histriophoca* would then be relegated to the rank of subgenera.

The Phocini have been divided by Chapskii (1955*a*) into two subtribes, the Phocina and the Histriophocina, an arrangement that was followed by King (1964) and Thenius (1969, 1972). According to these authors, the Phocina includes the genera *Phoca*, *Pusa*, and *Halichoerus* and the Histriophocina is made up of the genera *Histriophoca* and *Pagophilus*. These subdivisions agree with the present analysis provided that *Cystophora* is included in the Histriophocina (King (1966) clearly defined the phocine affinities of this genus). However, the taxon Histriophocina is not acceptable according to Article 36 of the *International Code of Zoological Nomenclature* and Cystophorina Gray, 1837, has priority over Histriophocina Chapskii, 1955. The Phocini could accordingly be divided into the subtribes Phocina and Cystophorina. This subdivision is probably pointless and, following the sequencing process of
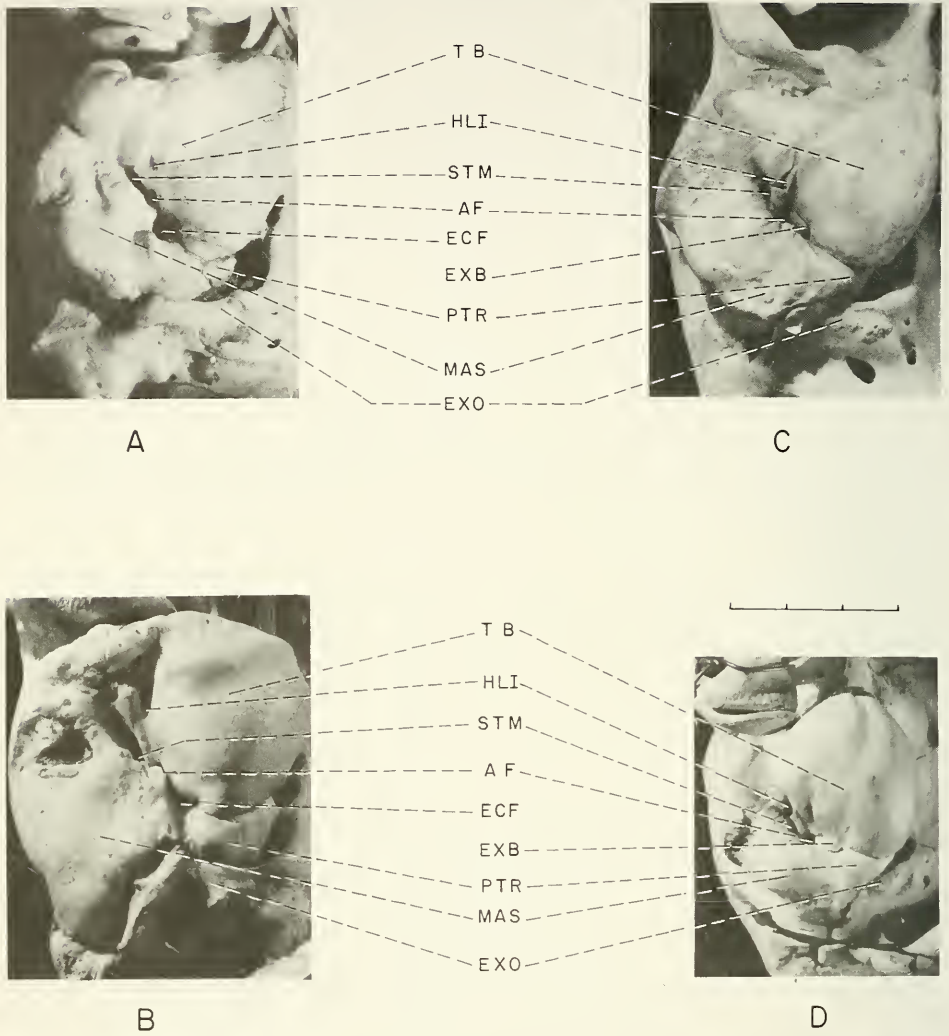
Fig. 6. Right auditory region of some Phocinae showing the auditory foraminae. A. *Pagophilus groendlandicus*. B. *Cystophora cristata*. C. *Phoca vitulina*. D. *Halichoerus grypus*. Af—auricular foramen; ECF—external cochlear foramen; EXB—expansion of the tympanic bulla which tends to obstruct the external cochlear foramen; EXO—exoccipital; HLI—hyoid ligament insertion; MAS—mastoid; PTR—petrosal; STM—stylomastoidian foramen; TB—tympanic bulla. Scale = 3 cm.

Nelson (1974), the Phocinae are divided here into three tribes: Erignathini, Phocini, and Cystophorini (Fig. 5).

This interpretation contrasts with that suggested by Arnason (1972) who stated that some phocids have a 32-chromosomal karyotype while all the others have 34 chromosomes. He concludes that the 32-chromosomal *Phoca*, *Pusa*, *Halichoerus*, *Histriophoca*, and *Pagophilus* represent a monophyletic group that excludes the 34-chromosomal *Cystophora*.

The phocine phylogeny presented here (Fig. 5) is based on living genera only and will have to be tested as more fossil phocine material is discovered.

THE MONACHINAE

This subfamily is divided into two groups on the basis of an apomorphy in the auditory region; the tympanic bulla tends to extend backward to cover the petrosal completely. The plesiomorphic condition among Phocidae is a petrosal partially visible outside the bulla. The validity of the apomorphy may be questioned since both *Potamotherium* and the primitive mustelid *Paragale* have a tympanic bulla completely covering the petrosal. Consequently, the plesio- morphic condition may in fact be apomorphic and vice versa. However, a functional interpretation justifies the former alternative.

Repenning (1972) pointed out that underwater hearing and pressure resis- tance are important adaptive factors related to modifications in the auditory region of seals. Underwater hearing is improved by an increase in the size of the promontorium (directional audition) and an inflation of the petrosal apex (auditory sensibility). Another way of improving underwater hearing is the opening of an external cochlear foramen, which suppresses all bony barriers between the round window and external environment. Thus, the auditory cells of the cochlea are separated from the water by flesh only, which creates a process somewhat similar to the lateral line organ of fishes (Repenning 1972). In addition, an external exposure of the petrosal, not completely covered by the bulla, increases the potential and the efficiency of hearing by bony conduc- tion of the vibrations that are transmitted to the cells of the cochlea directly by the petrosal. However, the presence of posteriorly exposed petrosal represents a deficiency in pressure resistance (the pressure resistance is directly connected to deep diving). In some monachines the increase in pressure resistance is obtained by a posterior projection of the bulla, which completely covers the petrosal, and by the development of a mastoid lip overlapping the posterior wall of the bulla (observed by Repenning & Ray 1977), and which obstructs the external cochlear foramen.

As noted by Repenning & Ray (1977), *Monachus* is regarded as the most primitive of living seals (and even more primitive than most known fossil seals), and the petrosal of this genus is visible in ventral view of the skull because it is not completely covered by the tympanic bulla (King 1966). An external cochlear foramen is also present (Fig. 7). The promontorium and the petrosal apex are less enlarged than in any other living or known fossil seals (Repenning
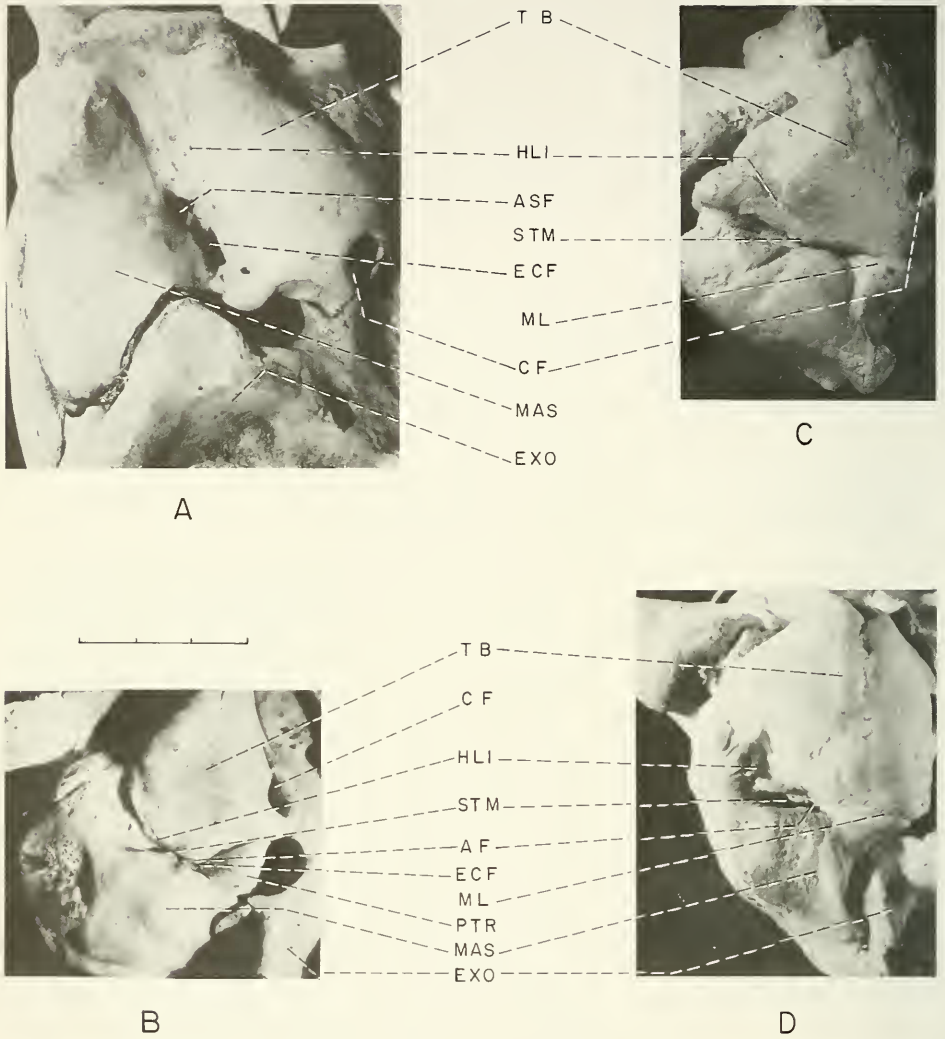
Fig. 7. Right auditory region of some monachines showing the auditory foraminae. A. *Mirounga leonina*. B. *Monachus monachus*. C. *Homiphoca capensis*. D. *Lobodon carcinophagus*. ASF—auriculo-stylomastoid foramen; CF—carotidian foramen; ML—mastoid lip which closes the external cochlear foramen (For other abbreviations, See Fig. 6.) Scale = 3 cm.

& Ray 1977). Thus, compared with other seals it seems that *Monachus* is likely to have poor underwater hearing, improved, however, by the presence of an external cochlear foramen and by a posteriorly exposed petrosal. These structures otherwise offer little resistance to high pressure and *Monachus* is, in fact, a littoral species and a shallow diver.

Except for some individual variations, the phocine seals have a posteriorly exposed petrosal and most of them have an opened, or partially opened, external cochlear foramen. The Phocini show a tendency toward closure of this foramen, but it is never hermetically obstructed as in some Monachinae. The phocine petrosal generally has an inflated promontorium and a swollen apex. Thus, the phocine auditory region is well adapted to underwater hearing (direction and sensibility), but with rather weak pressure resistance for a seal. This is in keeping with the fact that phocines are shallow divers (Kooyman & Andersen 1969; Van den Brink & Barruel 1971).

The condition observed in *Monachus* is very similar to that in *Cystophora*. In both genera the external cochlear foramen is located at the anterior extremity of a groove separating the mastoid bulla and the petrosal, the latter not being completely covered by the tympanic bulla. This striking similarity is here regarded as a symplesiomorphy. There are also slight differences between the auditory region of both genera. In *Monachus* the external cochlear foramen and the groove are always less marked than in *Cystophora*. In old individuals of *Monachus* the external cochlear foramen is sometimes almost obstructed by an expansion of the bulla. However, in *Cystophora* the bulla shows a slight tendency to extend backward and to cover the posterior part of the petrosal, while in *Monachus* the external part of the petrosal, at its limit with the bulla, shows a conspicuous thickening which apparently prevents any posterior projection of the bulla.

The Antarctic seals are divided into two tribes, the Miroungini trib. nov. (see p. 199) and the Lobodontini. The Miroungini include (*pro parte*) the elephant seals. In this group the bulla completely covers the petrosal but the external cochlear foramen is wide open, more so than in *Monachus*. The promontorium and the petrosal apex are well developed. Consequently, as in the phocines, the anatomy of the elephant seal indicates good underwater hearing but a rather poor ability for deep diving when compared with the other Antarctic seals. In fact, the elephant seals are littoral species and are not known to be deep divers (Kooyman & Andersen 1969; Bryden 1971).

The living Lobodontini include the four genera: *Hydrurga*, *Lobodon*, *Leptonychotes*, and *Ommatophoca*. They have a posterior projection of the bulla and the external cochlear foramen is completely obstructed by the development of a mastoid lip overlapping the posterior border of the bulla. The promontorium is considerably inflated and the apex of the petrosal is very swollen. Therefore, it seems that the Lobodontini are well adapted for both underwater hearing (direction and sensibility) and deep diving. Deep diving has been observed among living Lobodontini in the Weddell seal (*Leptonychotes*

weddelli) that can dive to a depth of 600 m (Kooyman 1966; Kooyman & Andersen 1969). The greatest diving depth observed for phocine seals is around 300 m and, generally speaking, it is no more than 100 m (Van den Brink & Barruel 1971).

However, a condition somewhat similar to that of the Lobodontini is present in *Erignathus*, a primitive phocine that exhibits some variability in the structure of its auditory region. In this genus the external cochlear foramen tends to disappear and the bulla very often covers the petrosal posteriorly. These two features are never as well marked and constant as in the Lobodontini and a mastoid lip is not present. *Erignathus* clearly shows the synapomorphies of the Phocinae, and the similarities observed sporadically between its auditory region and that of the Lobodontini are considered here as parallel apomorphies.

To sum up, the morphological stages representing the modifications of the auditory region of seals for aquatic adaptation can be illustrated by *Potamotherium*, *Monachus*, a phocine such as *Pagophilus*, and a lobodontine such as *Leptonychotes*. The auditory region of *Potamotherium* is already fairly specialized, which suggested to Tedford (1976) that this genus is related to the Phocidae (*s.s.*). Nevertheless, it also resembles the auditory region of the primitive mustelid *Paragale*. In *Potamotherium* as in otters, but in contrast to seals, the adaptation to life in water is not pronounced. As in the *Monachus*-like stage, early phocids must first have developed underwater hearing by the shrinking of the tympanic bulla, which exposes the posterior part of the petrosal underneath, and by the opening of an external cochlear foramen, which increases the bony transmission of vibrations by the petrosal and develops a mechanism similar to the lateral line in fish. Such primitive phocids were evidently shallow divers and must first have increased underwater hearing rather than pressure resistance. At the *Pagophilus*-like stage, the pressure resistance does not show much change, but the underwater hearing is improved by an inflation of the promontorium and of the petrosal apex. In the Lobodontini-stage the resistance to pressure is more developed than in any other seals. It is increased by the posterior projection of the bulla and the mastoid lip. The extreme development of the promontorium and the petrosal apex compensate for the obstruction of the external cochlear foramen in the function of underwater hearing.

It therefore appears that the posterior projection of the tympanic bulla and the obstruction of the external cochlear foramen represent apomorphies among the Phocidae. Thus, it is apparently justified to use the first characteristic in a phocid phylogeny as a synapomorphy of Lobodontini and Miroungini (trib. nov) which together represent the sister group of the Monachini. The latter group is characterized by an apomorphic tendency toward oblique implantation of the cheek teeth relative to the axis of the tooth row, a feature which is always more obvious in the mandible than in the maxilla (Fig. 8). This feature, also found in some phocines by convergence, is a consequence of the shortening of the tooth row.

The Monachini

The living Monachini are represented by one genus and three species, namely, *Monachus monachus*, *M. tropicalis*, and *M. schauinslandi*, which live respectively in the Mediterranean and on the Mauritanian coast, in the Caribbean, and around Hawaii. The fossil genera of this tribe are *Pristiphoca* and *Pliophoca*. Following Thenius (1950, 1952, 1969, 1972) and contrary to Ray (1976b), *Miophoca* Zapfe, 1937, is regarded here as a subgenus of *Pristiphoca*. *Palmidophoca callirhoe* Ginsburg & Janvier, 1975, which is known by only one cheek tooth, is here regarded as *incertae sedis* although it may be related to *Pristiphoca*, which it closely resembles. Moreover, Paratethyan monachines, *Monotherium? gaudini* and *Prophoca rousseaui* are regarded as *incertae sedis* and were not taken into account in this study.

Pristiphoca Gervais, 1859, differs from *Monachus* in having a more slender mandible and a longer femur. Two species of this genus are known, *P. vetusta* (Zapfe, 1937) from the Middle Miocene of Neudorf (Czechoslovakia), and *P. occitana* Gervais, 1859, from the Lower Pliocene of Montpellier (France). On the mandibles of both species the tooth obliquity is clear, but it is more marked in the younger species, which is consistent with this being an apomorphic character. Thenius (1952: 66, fig. 27) referred a metatarsal III to *P. vetusta* which is much longer and hence more specialized than that of *Monachus*. Consequently, *Pristiphoca* is unlikely to be the ancestor of *Monachus*. The cheek teeth obliquity is more pronounced and therefore more specialized in *P. occitana*   and *M. monachus* than in *M. tropicalis* and *M. schauinslandi*. However, the three species of *Monachus* are more similar to each other in respect of mandible and tooth robustness than to *P. occitana*. It follows that the development of oblique cheek teeth relative to the tooth row axis represents a general tendency of Monachini, having being acquired by parallelism in various lineages of this tribe. Nevertheless, it is also possible that the palates of *M. tropicalis* and *M. schauinslandi*, which are longer than that of *M. monachus* (hence giving more space to the teeth), allow for their readjustment. The condition of the teeth of the American species would not then be a plesiomorphy but a secondary specialization.

Pliophoca etrusca, from the Pliocene of northern Italy, is so similar to *M. monachus* that it was initially described by Ugolini (1902) as *M. albiventer* (= *M. monachus*). The material was redescribed by Tavani (1942a) and assigned to a new genus and species, *Pliophoca etrusca*. In other respects, Tavani (1942b) described and illustrated some monachine remains from the Palaeontological Museum of Florence (Italy). Among these fossils is a talus that was described and is identical to that of *P. etrusca*, and one mandible that fits the skull of the type specimen perfectly. All these specimens are from the same region and from the same deposits near Orciano and, as noted by Tavani (1942b), probably belong to *P. etrusca*. The differences from *Monachus* are slight, with *P. etrusca* having a more posterior orientation of the proximal condyle of the humerus, a greater and somewhat higher trochanter of the
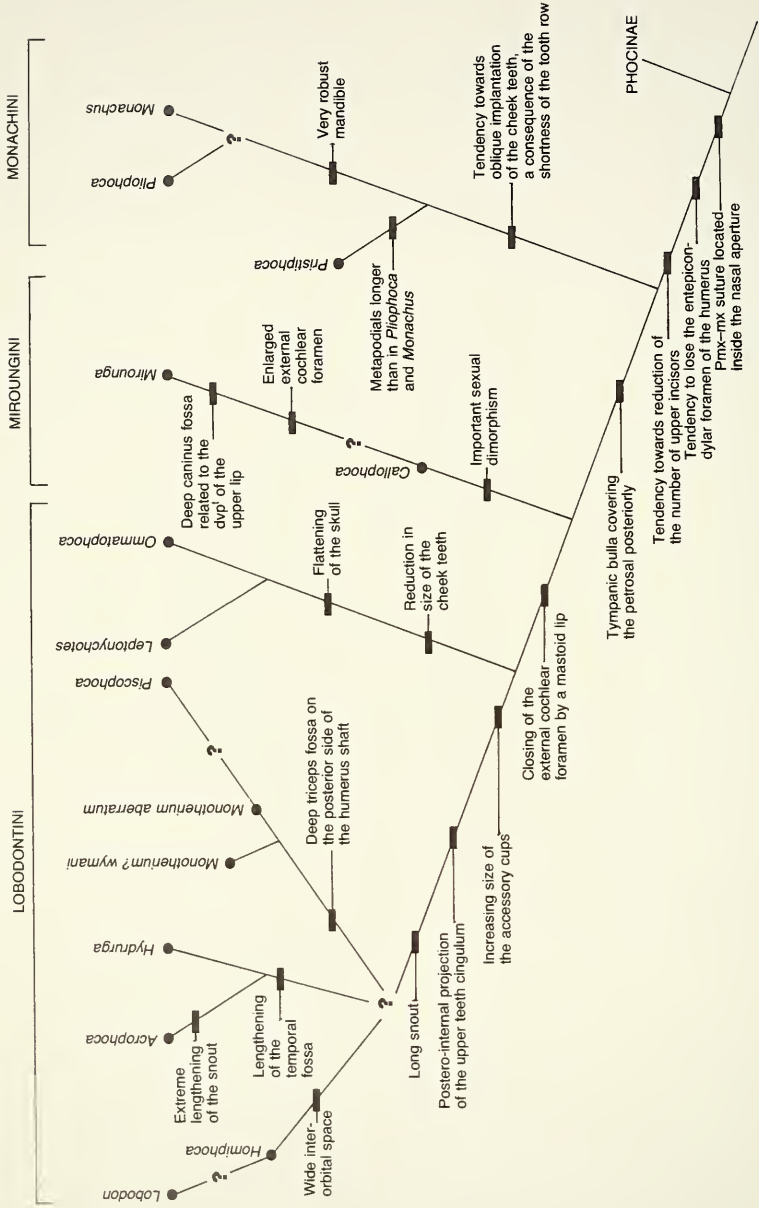
Fig. 8. Assumed relationships of the Monachinae.

femur, the femur narrower in its medial part, and the tibia shaft more flattened anteroposteriorly in its distal third.

The mandible of *Pliophoca* differs from that of *Pristiphoca* by its great stoutness. This feature, which it shares with *Monachus*, is regarded as a synapomorphy of *Pliophoca* and *Monachus*. The absence of any obvious characteristic excluding *Pliophoca* from the ancestry of *Monachus* and the close resemblance between the two genera suggests that the Orciano seal is a likely ancestor of the living monk seals. If this is indeed the case, then the lesser cheek teeth obliquity in *M. tropicalis* and *M. schauinslandi* relative to *M. Monachus* and *P. etrusca* represents a secondary specialization (see p. 197). There is, however, another problem. *M. schauinslandi* has an obvious plesiomorphy, that is, the tibia and the fibula of this species are articulated at their proximal extremities rather than fused as in all the other living seals (Ray 1976b). This feature may, therefore, exist in *P. etrusca*, but unfortunately the proximal extremities of these bones are unknown in the Italian species.

The Miroungini trib. nov.

The tribe is characterized by the posterior projection of the tympanic bulla and the absence of a mastoid lip closing the external cochlear foramen. It is represented by one living genus (*Mirounga*) and one fossil genus (*Callophoca*). *Palaeophoca nystii* van Beneden, 1859, was based on a cetacean tooth and therefore cannot be a phocid (Ray 1976b). Van Beneden (1887) illustrated under that name another cetacean tooth and several phocid bones. The latter should most probably be referred to *Callophoca obscura* (Ray 1976b).

The only part known of the skull of *Callophoca* is the auditory region (Ray 1976a, pl. 1, fig. 6). It apparently has no mastoid lip, but differs from that of *Monachus* by a clear tendency for the bulla to cover the petrosal posteriorly as in *Mirounga*. In this genus the external cochlear foramen differs from that of *Monachus* and the Cystophorini. In *Mirounga* the foramen is wide open and is not partially obstructed by an expansion of the bulla. This contrasts with the Phocinae in which there is a tendency for it to be closed. In *Mirounga* there seems to be a tendency to enlarge the external cochlear foramen but there is no pit (or groove) separating the mastoid and the petrosal, as observed in the Cystophorini and *Monachus* (see p. 191). Moreover, in *Mirounga* the auricular foramen, through which the auricular branch of the nerve X passes, very often joins the stylomastoid foramen to form an auriculostylomastoid foramen. In all the other seals the auricular foramen is located posteromedially to the stylomastoid foramen. Thus, the characteristics of the auditory region of *Mirounga* differ from those of *Monachus* and the Cystophorini. The tendency for enlargement of the external cochlear foramen apparently represents an apomorphy of *Mirounga*.

Since the skull of only one member of the tribe is known (*Mirounga*) the recognition of synapomorphies characterizing the group is difficult. The apomorphies of *Mirounga* could be at generic rather than tribal level. However,

Ray (1976*b*) observed a feature (apparently apomorphic) that would seem to indicate a close relationship between *Mirounga* and *Callophoca*. This latter genus is represented in Europe (Belgium) and in North America (U.S.A.) by two species, *C. obscura* and *C. (= Mesotaria) ambigua*. The latter is much larger than the former, but they are otherwise very similar, and Ray (1976*b*) suggests that this difference could be reasonably explained by sexual dimorphism. Since *Mirounga* is the only living phocid that exhibits marked sexual dimorphism, this could represent an amomorphy characterizing the Miroungini.

The suggested relationship of *Callophoca* to *Mirounga* was also made on the basis of striking similarities between the femora and humeri of both genera, although the apomorphy of these features is not demonstrated. These bones of the two genera are similar to those of *Monachus*, although they differ from this genus in the following respects:

(i) the humeri of *Callophoca* and *Mirounga* are more twisted in lateral view, they have a more proximally orientated condyle, a longer deltoid crest and a better developed epicondylian ridge,

(ii) the femora of *Callophoca* and *Mirounga* have a more globular proximal condyle, a lower trochanter and a wider distal extremity.

There are no known features that contradict the hypothesis that *Callophoca* is ancestral to *Mirounga*.

A provisional diagnosis of Miroungini trib. nov. is: Monachinae, characterized by marked sexual dimorphism and in which the auditory region shows a posterior projection of the tympanic bulla but without a mastoid lip obstructing the external cochlear foramen as observed in Lobodontini.

The Lobodontini

This group is distinguished by a posterior projection of the tympanic bulla and a mastoid lip. The living representatives can be divided into two groups (Hendey 1972; De Muizon & Hendey 1980). They are:

1. The *Ommatophoca–Leptonychotes* group, which is characterized by the following apomorphic features:

(i) flattening of the skull,
(ii) shortening of the snout,
(iii) reduction of the cheek teeth and of their accessory cusps.

The only known representatives of this group are the living genera *Ommatophoca* and *Leptonychotes*.

2. The *Lobodon–Hydrurga* group, which have the following synapomorphies:

(i) relatively high skull,
(ii) lengthening of the snout,
(iii) relatively large cheek teeth, with an emphasis in the size and number of the accessory cusps.

(iv) postero-internal projection of the cingulum of the upper cheek teeth, on which a well-defined postero-internal cusp is almost always developed.

This group is composed of two living genera, *Lobodon* and *Hydrurga*, and four known fossil genera, *Monotherium*, *Homiphoca*, *Acrophoca*, and *Piscophoca*.

The genus *Monotherium*, usually regarded as an ancestral form of the living monk seals, is here referred to the Lobodontini. This is based on the fact that *Monotherium? wymani* has a posterior projection of the bulla and a mastoid lip (Ray 1976*a*). As already stated concerning *Piscophoca pacifica* (De Muizon 1981*b*), all the similarities between *Monotherium* and *Monachus* are most probably to be considered as symplesiomorphies. Although the characters of the *Lobodon–Hydrurga* group could not be observed in *Monotherium*, the close relationship of this genus to *Piscophoca pacifica* (De Muizon 1981*b*) suggests that *Monotherium* belongs to this group.

Homiphoca was suggested by De Muizon & Hendey (1980) to be on the lineage leading to *Lobodon* on the basis of the following supposed synapomorphies:

  (i) the relatively wide interzygomatic bridge of the frontal,
 (ii) the appreciable height of the M_1,
(iii) the tendency for the presence of numerous accessory cusps strongly recurved towards the main cusps.

This relationship between *Homiphoca* and *Lobodon* was suggested because there are no obvious characteristics that preclude this hypothesis, while they share some common features that can be regarded as apomorphic.

Acrophoca is distinguished by the extreme length and tapering of its snout. In this respect it is more specialized than *Lobodon* and *Hydrurga* and cannot be directly ancestral to either genus. It does, however, have two apomorphic characters in common with *Hydrurga* that separate them from the other Lobodontini. They are:

  (i) the considerable length of the temporal fossa,
 (ii) the sagittal crest that is more developed than in any other monachine.

Thus, *Acrophoca* could represent a branch from the *Hydrurga* lineage.

Piscophoca pacifica is apparently a descendant of *Monotherium* (De Muizon 1981*b*). These two seals share a feature unique among the known phocids, that is, the posterior border of the proximal extremity of the humerus shaft has a very deep fossa where the triceps brachii (caput mediale) is partially inserted. Of the two species of *Monotherium* whose humerii are known, *M. aberratum* is the most likely ancestor for *Piscophoca pacifica*. This interpretation confirms the assignment of *Monotherium* to the Lobodontini and to the *Lobodon–Hydrurga* group.

Satisfactory apomorphic features to link the lineages *Homiphoca–Lobodon*, *Acrophoca–Hydrurga* and *Monotherium–Piscophoca* were not found and there are therefore three possibilities that can be considered.

Discussion

Repenning *et al.* (1979) have suggested a phocid phylogeny based upon biogeographic groups, but without precise information about the genera included in each branch. The phocines are divided into two groups: the Atlantic–Arctic group and the Paratethyan group. However, the genus *Pusa* (considered by the authors as a subgenus of *Phoca*) is very likely a descendant of the Paratethyan seals (such as '*Phoca*' *pontica* or '*Phoca*' *panonica*). It was also concluded earlier that *Pusa* is closely related to *Phoca*, both genera being, at least partially, Atlantic–Arctic seals (see p. 188). Consequently, the relationships of those two groups are much more complex and their phylogenetic homogeneity is not established. Moreover, the Paratethyan seals have not all been proved to be phocines and '*Monotherium*' *maeoticum* may well be a monachine.

Repenning *et al.* (1979) divide the monachines into a Hawaiian group, a Caribbean–Atlantic group and an Antarctic group. Once again, viewed in relation to the phocid phylogeny suggested here, these biogeographic groups are very heterogeneous. For example, the Caribbean–Atlantic group includes such genera as *Monotherium* and *Callophoca* (which are clearly related to the Antarctic seals), and *Monachus* and *Pliophoca*, the latter obviously related to the monk seals. This group, therefore includes representatives of the three tribes of Monachinae defined here. The Hawaiian Islands group, which includes the living species *Monachus schauinslandi*, is defined merely by geographic isolation, associated with the persistence of plesiomorphic features in *M. schauinslandi* such as the articulated tibia and fibula and the primitive morphology of the petrosal (Repenning & Ray 1977). In fact, one synapomorphy of both the Caribbean–Atlantic group and the Antarctic group could separate the Hawaiian Islands group, that is, the presence in the former two of a tibia and fibula fused at their proximal extremity. It can, therefore, be argued that the Hawaiian monk seal does not belong to the genus *Monachus* but must be assigned to a new genus. This is not advocated because that synapomorphy is a feature that can be ascribed to convergence. For example, Repenning & Tedford (1977) record an Otariidae (*Thalassoleon*) whose tibia and fibula are articulated, whereas all the living otariids have fused tibiae and fibulae. This feature is also found in some Xenarthra and reflects a strengthening of the limb for vigorous use.

A phylogeny based upon assumed apomorphic features is here preferred to one based on geographic groupings.

PHOCID PALAEOBIOGEOGRAPHY

McLaren (1960*a*), Hendey (1972), Thenius (1972), Ray (1976*a*), and Repenning *et al.* (1979) have discussed phocid palaeobiogeography, but some points concerning monachine dispersal are re-examined in the light of the phylogeny presented here.

NORTHERN ORIGIN OF MONACHINES

The authors cited above consider that the origin of all phocids, including the monachines, was in the North Atlantic, where most of the known fossil representatives of this family are found. The northern monachines are from at least four fossil genera, namely, *Monotherium*, *Callophoca*, *Pristiphoca*, and *Pliophoca*. *Monotherium* is recorded from the Middle and Upper Miocene of North America and the Upper Miocene of Belgium. *Callophoca* is from the Pliocene of Virginia (U.S.A.) and of Belgium. *Pliophoca* (Pliocene) and *Pristiphoca* (Middle Miocene and Lower Pliocene) are European genera. The following points support the theory of the northern origin of monachines:

  (i) *Monotherium aberratum*, which is found on the eastern coast of U.S.A., seems the most likely ancestor of *Piscophoca pacifica*. This implies a southern migration of this lineage,

  (ii) *Callophoca*, a northern genus (U.S.A., Belgium), is the likely ancestor of *Mirounga*, which is represented at least partially in the southern hemisphere: *M. leonina* lives in the Antarctic waters, while *M. angustirostris* breeds along the Californian coast.

MODE OF DISPERSAL

Hendey (1972: 103 fig. 1) suggests a dispersal of the monachines along the transatlantic and coastal currents. It is highly probable that currents did play an important role in the migrations of marine mammals such as phocids. Nevertheless, it seems unlikely that the coastal currents were significant because the phocids are very dependent on the land and their dispersal along the coasts might have been independent of the direction of the currents. The situation in respect of transatlantic currents is very different. It is most unlikely that seals could have crossed the Atlantic swimming against the current, and it follows that these currents played a prominent part in the dispersal of the monachines (De Muizon & Hendey 1980).

ORIGIN AND DISPERSAL ROUTES OF MONACHINE TRIBES.

The Monachini

All the living and fossil representatives of this tribe are located in warm waters and in low latitudes.

The presence of monk seals (*Monachus*) in the Mediterranean (*M. monachus*), in the Caribbean (*M. tropicalis*), and around Hawaii (*M. schauinslandi*) indicates at least one crossing of the Atlantic by this group. The apparent preference of the Monachini for warm waters makes it highly probable that the crossing was in the southern North Atlantic, by way of equatorial currents from east to west. It follows that the original homeland of the Monachini must have been in Europe.

Several factors support this hypothesis. Firstly, the three described species of fossil Monachini are from southern Europe, while the Yorktown Formation

in the south-eastern United States, where the phocid remains are very abundant, is apparently devoid of Monachini. In addition. if this group originated in North America, their crossing of the Atlantic could have been accomplished only by a 'palaeo-Gulf Stream' which would have carried them towards northern Europe. However, no Monachini are known in the Antwerp sands (Belgium), and seals of the 'faluns de la Touraine et de l'Anjou' (Ginsburg & Janvier 1971, 1975) have yet to be established as Monachini because they are known only by isolated teeth.

The most probable migration route for the Monachini would, therefore, have been southward following the north African coast (Mauritania and Senegal) and crossing the Atlantic by way of the equatorial currents to reach the coast of Brazil and continuing north to the Caribbean. It is possible, therefore, that the common ancestor of the living species of *Monachus* that gave rise to *M. monachus* in the Mediterranean migrated eastward by this route, giving rise in the Caribbean to the ancestors of the living *M. tropicalis* and *M. schauinslandi*. It is worth noting that these two species are closer to each other than either is to *M. monachus* (King 1956; Scheffer 1958). *M. schauinslandi*, or its ancestors, would then have passed into the Pacific Ocean before the emergence of the Panama Isthmus, about 3,5 to 4 m.y. ago (see Beggren & Hollister 1974). The Phocidae might have been the last marine animals to cross this route because of their ability to move on dry land.

An undescribed monachine from Sud-Sacaco (Peru), which is known only by mandibles and some postcranial bones, has characteristics that suggest it belongs to the Monachini. Because of the slenderness of its mandible, it is closer to *Pristiphoca* than to *Monachus* and its size is similar to that of *P. vetusta*. As in that species, the metapodials are proportionally longer than those of *Monachus*; the Sud-Sacaco Monachini cannot, therefore. be ancestral to any of the living monk seals. In addition, it must have entered the Pacific Ocean before 4 or 5 m.y. ago, the assumed age of the Sud-Sacaco fauna (De Muizon & Bellon 1980). Therefore, there could have been two migrations from east to west, the first one giving rise to the Monachini of Sud-Sacaco, and the second to *M. tropicalis* and *M. schauinslandi*.

The assumed Monachinae of the Paratethys, such as '*Monotherium*' *maeoticum* Nordman. 1860, and '*Phoca*' *bessarabica* Simionescu. 1925, are possibly Monachini, but because they are so poorly known they are listed here as *incertae sedis* (table 1).

Ray (1976b) and Repenning *et al.* (1979) have proposed the idea that *Monachus* re-invaded the Mediterrenean from the Atlantic after the Messinian crisis. In fact. the complete desiccation of the Mediterranean is now seriously questioned and the main defendants of this idea (Hsü *et al.* 1973) have had to moderate their interpretation in face of the strong opposition of several geologists and palaeontologists working on the Mediterranean littoral. Many authors now regard the idea of a complete desiccation of the Mediterranean basin as somewhat extremist and simplistic (Montenat 1977; Gaudant 1978;

TABLE 1
Phocid classification.

Family	Subfamily	Tribe	Genera and species
PHOCIDAE	PHOCINAE	Erignathini	*Erignathus*
		Phocini	*Phoca* *Pusa* *Halichoerus*
		Cystophorini	*Cystophora* *Pagophilus* *Histriophoca*
		Undetermined tribe	*Phocanella** *Platyphoca** *Leptophoca** *Gryphoca** *'Phoca' vindoboniensis** *'Phoca' pontica**
	Incertae sedis		*Prophoca rousseaui** *'Monotherium' meoticum** *'Monotherium' gaudini** *'Phoca' bessarabica**
	MONACHINAE	Monachini	*Pliophoca** *Pristiphoca** *Monachus*
		Miroungini	*Callophoca** *Mirounga*
		Lobodontini	*Monotherium** *Homiphoca** *Acrophoca** *Piscophoca** *Lobodon* *Hydrurga* *Leptonychotes* *Ommatophoca*

*Fossil genera and species

Busson 1979; Sorbini & Tirapelle Rancan 1979; Roep & Van Harten 1979, Rouchy 1979; Montenat *et al.* 1980). It seems highly probable that even during the most critical period of the Messinian event some lakes and lagoons, at least, persisted on the periphery of the Mediterranean; this does not contradict the possibility of a complete desiccation in some basins of the Mediterranean. Hence, it seems quite possible and more satisfactory to consider that the pre-Messinian Monachini never disappeared from the Mediterranean, giving rise there to *Pliophoca* and *Monachus* during the Pliocene.

The Miroungini

The living Miroungini occur in Subantarctic waters (*Mirounga leonina*) and on the Californian coast (*M. angustirostris*), while the fossil representatives of this tribe, *Callophoca obscura* and *C. ambigua*, which are very probably conspecific, have been found in Europe (Belgium) and North America (east coast of U.S.A.). The European origin of this tribe cannot be substantiated. The presence of *Callophoca* in northern Europe and the fact that it was not found in southern Europe suggest a crossing of the Atlantic Ocean by way of the northern North Atlantic. The Gulf Stream, which crosses the Atlantic in that zone, flows from west to east and it is therefore possible that *Callophoca* crossed the Atlantic Ocean in this direction. On the other hand, Repenning *et al.* (1979) have expressed the opinion that the primitive monachines were probably warm-water animals like the living monk seals and that the adaptation to Arctic and Antarctic conditions is a recent development among the phocids. This observation suggests a migration via the southern North Atlantic by way of the equatorial currents from east to west. Both migration routes are thus possible.

Since *Callophoca* is the likely ancestor of *Mirounga*, it is possible that the former entered the Pacific Ocean during the Early Pliocene to give rise here to the *Mirounga* lineage, with *M. angustirostris* in the north and *M. leonina* in the south. The latter species, which is now rare on the Pacific coast of South America, was common there two centuries ago, the type locality of the species being Juan Fernandez Islands (Chile) where they have since been exterminated (Scheffer 1958).

The Lobodontini

As with the Miroungini, the original homeland of the Lobodontini is uncertain. In the Northern Hemisphere, Lobodontini have been found in the Upper Miocene of Belgium: they are *Monotherium aberratum*, *M. delognii* and *M. affine* (very probably conspecific with *M. delognii*, see Ray 1976*b* and De Muizon 1980*a*). In northern Italy. Guiscardi (1871–3) described *Phoca gaudini* from the Miocene of the Abbruzes. This species was referred to *Monotherium* by Sarra (1930), Ginsburg & Janvier (1975), and Ray (1976*b*). The cheek teeth of *M.? gaudini* are not obliquely implanted as they are in the Monachini, which suggests that it does not belong to this group. However, the auditory region that is necessary to recognize a Lobodontini is not known and. following Ray's (1976*b*) opinion, this species is here regarded as *incertae sedis*. In North America, *Monotherium? wymani* comes from the Calvert Formation (Middle Miocene from Virginia, U.S.A.) and *M. aberratum* is known in the Gay Head Green Sand of St Marys Formation (Late Miocene from Maryland. U.S.A.).

There are two possible centres of origin for the Lobodontini. namely, Europe and North America. In the case of the former, the North Atlantic would have been crossed in the south by way of equatorial currents (east to west), whereas in the case of a North American origin, the crossing would have
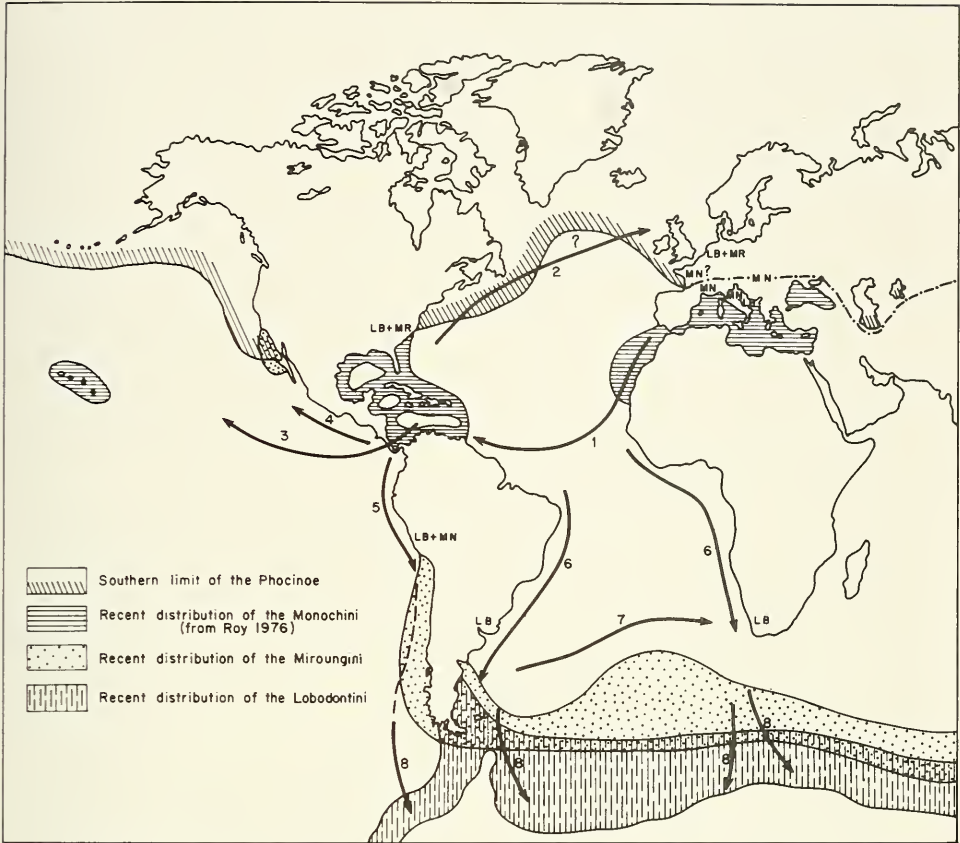
Fig. 9. Distribution of recent Monachinae and probable ways of dispersal of the monachines. MN—fossil Monachini; MR—fossil Miroungini; LB—fossil Lobodontini.

1. Migration of the Monachini (and probably all the Monachinae) by way of equatorial currents.
2. Possible west to east migration for the Miroungini and the Lobodontini (in the case of a North American origin for these two tribes).
3. Migration of the Monachini to Hawaiian Islands (*Monachus schauinslandi*).
4. Settlement of the Miroungini on the Californian coast (*Mirounga angustirostris*).
5. Southward migration of the Lobodontini that settled on the Peruvian coast in the Upper Miocene–Lower Pliocene. Probable southward migration of the Miroungini.
6. Probable ways of migration of the Lobodontini in the South Atlantic.
7. Possible migration of Argentinian monachines to South Africa by way of the Antarctic current.
8. Establishment of the Lobodontini in Antarctic waters.
(N.B. See Addendum.)

been by way of the Gulf Stream (west to east) in the northern North Atlantic. Lobodontini entered the Pacific before 4 to 5 m.y. ago and are represented on the Peruvian coast in the Lower Pliocene (Sud-Sacaco). It is also possible that the Lobodontini migrated along the Atlantic coast of South America to Argentina (assuming that the monachine teeth described by Frenguelli (1922) are in fact Lobodontini) and from there, crossing the South Atlantic by way of the west-to-east Antarctic current, settled in South Africa where thay are represented by *Homiphoca capensis* (Hendey 1972).

However, a study of undescribed monachine material from the Middle Miocene of Argentina (De Muizon & Bond 1982), clearly states that no close relation exists between *Homiphoca capensis* and the Argentinian phocid. The latter belongs to a different lineage and probably must be classified in the Monachini; however, this is not proved, and no skull of the Argentinian form is known. Considering this relationship, the authors stated that a monachine migration from the Argentinian coast to South Africa is very improbable and suggested that the ancestor of *Homiphoca* might have migrated southward along the Atlantic coast of Africa. This was also stated by De Muizon (1982).

To sum up, the migration southward of the Lobodontini is certain only on the Pacific coast of South America. In the Atlantic Ocean it might have been along the African or South American coast, or both. Repenning *et al.* (1979, fig. 2) suggest that the only southward migration for the Lobodontini was along the Pacific coast of South America. As stated by De Muizon (1981*c*) it seems highly improbable that this group of North Atlantic origin would not have used the South Atlantic in its migration to the Antarctic.

CONCLUSIONS

The Phocidae originated in the Northern Hemisphere. The phocine seals established themselves in the North Atlantic Ocean and spread to the Pacific, crossing the Arctic Ocean probably during the Pleistocene (Ray 1976*b*), while the monachines migrated southward. The Monachini stayed in warm subtropical and tropical waters, while the Lobodontini and Miroungini (except for *M. angustirostris*) reached Antarctic waters during the Pliocene. The original homeland of the Phocidae is rather difficult to determine because of the poor fossil record of early forms, but indications are that it was in Europe.

Phocid remains are fairly abundant in Europe (Paratethys and Antwerp Basin) and in North America (Virginian and Carolinian coasts). The oldest known fossil phocids are about 15 m.y. old (Middle Miocene) and are known in Europe and North America; *Potamotherium* (Semantoridae) comes from Early and Middle Miocene levels of Europe. The Phocidae, therefore, most probably appeared during the Oligocene. During this period, central Europe was a complex mosaic of intracontinental basins, an environment favourable for the acquisition of the aquatic adaptations. Moreover, the Semantoridae (*Potamotherium* and *Semantor*) are apparently exclusively from Europe and western Asia,

the American evidence for these genera being very doubtful. A European origin for the Phocidae is far from being proven, but it is in accord with the known fossil record of the family and would satisfactorily explain many problems of phocid palaeontology. For example, the phocine features of the ? monachines of the Paratethys can be explained as plesiomorphic features common to the Phocinae and Monachinae and these monachines could, therefore, stem from a very primitive monachine lineage, geographically close to the centre of dispersal of the Phocidae. Thus, from the centre of Europe during the Oligocene, the first phocids would have reached the North Sea and the place of the future Paratethys and the Mediterranean. The Paratethys appears at the Early Miocene with the closure of the Ouralian, Trans-Polish, and Alsatian Straits, which separated it from the Boreal seas (Pomerol 1973). Later, two phocid populations were isolated and evolved separately in the North Sea and in the Mediterranean–Paratethys.

Phocinae and Monachinae were most probably present in both regions during the Miocene. This would seem to indicate that, before the separation of the two geographical areas during the Early Miocene, the subfamilies of Phocidae were already differentiated. In the case of the monachines, this geographical separation would have given rise in the north to the Miroungini and Lobodontini and in the south to the less specialized Monachini. This hypothesis has to be tested by the discovery of more complete material in southern Europe. During the Early Miocene the northern population of European phocids might have migrated to the Americas by way of the European west coast and the equatorial currents of the Brazilian coast. They would then have colonized the Caribbean and the eastern seaboard of North America. As noted by Repenning *et al.* (1979), the Miocene phocids were apparently adapted to relatively warm water conditions and this makes an equatorial crossing of the North Atlantic more likely. Moreover, a northern crossing of the North Atlantic would imply that they might have swum against the Gulf Stream, which, as stated previously, is improbable. In the Caribbean and on the coast of North Carolina and Virginia, the monachines apparently prospered, whereas the phocines were much less abundant (Repenning *et al.* 1979). During the Miocene and the Pliocene, the southern population of European monachines apparently followed the same route to reach the Americas (see p. 204). The Lobodontini and the Miroungini then passed into the Pacific and migrated to the south along the Pacific coast of South America, but the Atlantic coasts of South America and Africa were also very probable routes of southward migration for these monachines (p. 208). Most of the Monachini and all the Phocinae remained in the Northern Hemisphere.

This interpretation of phocid dispersal is rather speculative, for example, it is not demonstrated that all the monachines of southern Europe are Monachini. Nevertheless, considering the scarcity of fossil phocid material it is thought, as does Hendey (1972), that it is preferable to speculate a little than to wait for hypothetical new discoveries.

Unclassifiable specimens are common in the fossil phocid record; most of the specimens are isolated bones or fragments with very few skull elements. Even when the remains are almost complete (e.g. *Piscophoca pacifica*, *Acrophoca longirostris*, *Pliophoca etrusca*, *Homiphoca capensis*), the phylogenetic relationships may still be difficult to determine. Consequently, all hypotheses on the phylogeny and dispersal of the Phocidae could be radically changed by new discoveries of well-preserved material from critical areas. This was clearly indicated by Ray (1976*b*: 404).

ADDENDUM

This paper was already prepared when Schmidt-Kittler (1981) published his interpretation of musteloid and procyonoid relationships. In the latter work *Potamotherium* is excluded from the Musteloidea (*sensu* Tedford 1976) and regarded as a form close to the procyonids without any precise relationship being defined. Nevertheless, the affinities of *Potamotherium* indicated in the present paper are confirmed elsewhere (De Muizon in press) by some anatomical evidence mainly in the auditory region.

In Figure 9 the Argentinian monachines are regarded as Lobodontini. In a study presenting some new monachine material from Argentina, De Muizon & Bond (1982) stated that these phocids should very probably be related to the Monachini; unfortunately this information came too late to allow the modification of Figure 9. The authors also stated that, considering this interpretation, a monachine migration from Argentina to South Africa was highly improbable (see p. 208).

ACKNOWLEDGEMENTS

REFERENCES

ARNASON, U. 1972. The role of chromosomal rearrangement in mammalian speciation, with special reference to Cetacea and Pinnipedia. *Hereditas* **70**: 113–118.
BERGGREN, W. A. & HOLLISTER, C. D. 1974. Paleogeography, paleobiogeography and the history of circulation in the Atlantic Ocean. *In:* HAY, W. W. *ed. Studies in paleo-oceanography. Spec. Publs. Soc. Paleont. Miner. Tulsa* **20**: 126–186.
BRYDEN, M. M. 1971. Myology of the southern elephant seal *Mirounga leonina* (L.) *In:* BURT, W. H. *ed. Antarctic Pinnipedia. Antarct. Res. Ser. Washington* **18**: 109–140.
BURNS, J. J. & FAY, F. H. 1970. Comparative morphology of the skull of the ribbon seal *Histriophoca fasciata* with remarks on systematics of Phocidae. *J. Zool.* **161**: 363–394.
BUSSON, G. 1979. Le 'géant salifère' Messinien du domaine méditerranéen: interprétation génétique et implications paléogéographiques. VIIth Intern. Congr. Medit. Neog., Athens 1979. *Annls. géol. Pays hell.* (h.s.): 227–238.

CHAPSKII, K. K. 1955a. An attempt at revision of the systematics and diagnoses of seals of the subfamily Phocinae. *Trudȳ zool. Inst. Leningr.* **17**: 160–199 (in Russian).

CHAPSKII, K. K. 1955b. On the problem of the History of the development of the Caspian and Baikal seals. *Trudȳ zool. Inst. Leningr.* **17**: 200–216 (in Russian).

DOUTT, J. K. 1942. A review of the genus *Phoca. Ann. Carneg. Mus.* **29**: 61–125.

FISCHER, E. M. 1939. Habits of the southern sea otter. *J. Mammal.* **20**: 21–36.

FRENGUELLI, J. 1922. *Prionodelphis rovereti*, un representante de la familia 'Squalodontidae' en el Paranense Superior de Entre Ríos. *Boln Acad. nac. Cienc. Córdoba* **25**: 491–500.

FRIANT. M. 1947. Recherche sur le fémur des Phocidae. *Bull. Mus. r. Hist. nat. Belg.* **23**: 1–51.

GAUDANT, J. 1978. Signification bathymétrique, paléoclimatologique et paléogéographique de l'ichthyofaune marine du Miocène terminal de la Méditerranée occidentale. Remarques préliminaires. *Bull. Mus. natn. Hist. nat. Paris* **518**: 137–148.

GERVAIS, P. 1859. *Zoologie et paléontologie française.* Paris: Arthus Bertrand.

GILL. T. 1873. The ribbon seal of Alaska. *Am. Nat.* **7**: 178–179.

GINSBURG, L. & JANVIER, PH. 1971. Les Mammifères marins des faluns miocènes de la Touraine et de l'Anjou. *Bull. Mus. natn. Hist. nat. Paris* **22**: 161–195.

GINSBURG, L. & JANVIER, PH. 1975. Les Mammifères marins des faluns de la Touraine et de l'Anjou, gisments et paléontologie. *Bull. Soc. Etud. scient. Anjou* **9**: 73–96.

GRAY, J. E. 1837. Description of some new or little known Mammalia principally in the British Museum collection. *Mag. nat. Hist.* (n.s.) **1**: 577–587.

GRAY, J. E. 1844. The seals of Southern Hemisphere. *In: The Zoology of the Voyage of H.M.S. 'Erebus' & 'Terror' . . . during the years 1839 to 1843* **1–8**, pls 1–10, 14–17. London: Richardson & Gray.

GRIGORESCU, D. 1976. Paratethyan seals. *Syst. Zool.* **25**: 407–419.

GUISCARDI, G. 1871–3. Sopra un teschio fossile di foca. *Atti, Accad. Sci. fis. mat., Napoli* **5**: 1–8.

HELBING, H. 1921. Zur Skelettrekonstruktion eines oberoligocänen Fischotters. *Verh. schweiz. naturf. Ges.* (101e Session Neuchatel) **1920**: 209–210.

HENDEY, Q. B. 1972. The evolution and dispersal of the Monachinae (Mammalia, Pinnipedia). *Ann. S. Afr. Mus.* **59**: 99–113.

HENDEY, Q. B. & REPENNING, C. A. 1972. A Pliocene phocid from South Africa. *Ann. S. Afr. Mus.* **59**: 71–98.

HOWELL, A. B. 1929. Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). *Proc. U.S. natn. Mus.* **73**: 1–142.

HSÜ, K. J., CITA, M. B. & RYAN, W. B. F. 1973. The origin of the Mediterranean evaporites. *Initial reports of the D.S.D.P., Washington*: U.S. Government Printing Office **13**: 1203–1231.

KELLOGG, R. 1922. Pinnipeds from Miocene and Pleistocene deposits of California. *Univ. Calif. Publ. geol. Sci.* **13**: 23–132.

KING, J. E. 1956. The monk seals (genus *Monachus*). *Bull. Br. Mus. nat. Hist.* (Zool.) **3**: 201–256.

KING, J. E. 1964. *Seals of the world.* London: British Museum (Nat. Hist.).

KING, J. E. 1966. Relationships of the hooded and elephant seals genera *Cystophora* and *Mirounga. J. Zool.* **148**: 385–398.

KIRPICHNIKOV, A. A. 1955. New data on *Semantor. Vop. Geol. Azii* **2**: 810–814 (in Russian).

KIRPICHNIKOV, A. A. 1964. On the origin of the Caspian seals. *Byull. mosk. Obschch. Ispyt. Prir. Otd. Biol.* **69**: 136–139 (in Russian).

KOOYMAN, G. L. 1966. Maximum diving capacities of the Weddell seal (*Leptonychotes weddelli*). *Science* **151**: 1553–1554.

KOOYMAN, G. L. & ANDERSEN, H. T. 1969. Deep diving. *In:* ANDERSEN, H. T. *ed. The Biology of marine mammals*: 65–94. New York, London: Academic Press.

LINNAEUS, K. VON 1758. *Systema naturae* **1**: 1–532. 10th ed. Stockholm: Laurentii Salvii.

MCLAREN, I. A. 1960a. On the origin of the Caspian and Baikal seals and the paleoclimatological implication. *Am. J. Sci.* **258**: 47–65.

MCLAREN, I. A. 1960b. Are the Pinnipedia biphyletic? *Syst. Zool.* **9**: 18–28.

MCLAREN, I. A. 1975. A speculative overview of phocid evolution. *In:* RONALD, K. & MANSFIELD, A. W. *eds. Biology of the seal. Rapp. P.-V. Réun. Cons. int. Explor. Mer* **169**: 43–48.

MIVART, ST. G. 1885. Notes on the Pinnipedia. *Proc. zool. Soc. Lond.* **1885**: 484–500.

MITCHELL, E. 1967. Controversy over diphyly in Pinnipeds. *Syst. Zool* **16**: 350–351.
MITCHELL, E & TEDFORD, R. H. 1973. The Enaliarctinae, a new group of extinct aquatic Carnivora and a consideration on the origin of the Otariidae. *Bull. Am. Mus. nat. Hist.* **151**: 201–284.
MONTENAT, C. 1977. Les bassins Néogènes du Levant d'Alicante et de Murcia (cordillères bétiques orientales—Espagne). Stratigraphie, Paléogéographie et Evolution dynamique. *Docums Lab. Géol. Fac. Sci. Lyon* **69**: 1–345.
MONTENAT, C., OTT D'ESTEVOU, P., PLAZIAT, J.-C. & CHAPTEL, J. 1980. La signification des faunes marines contemporaines des évaporites messiniennes dans le Sud-Est de l'Espagne. Conséquences pour l'interpratation des conditions d'isolement de la Méditerranée occidentale. *Géol. médit.* **7**: 81–90.
MUIZON, CH. DE. 1979. Contribution à l'étude systématique, anatomique et fonctionnelle des Phocidae pliocènes de la Formation Pisco (Pérou). Considérations générales sur la phylogénie et la paléobiogéographie des Phocidae. Thèse, Univ. Pierre-et-Marie-Curie, Paris.
MUIZON, CH. DE. 1981a. Les Vertébrés fossiles de la Formation Pisco (Pérou). Première partie: deux nouveaux Monachinae (Phocidae, Mammalia) du Pliocène de Sud-Sacaco. *Trav. Inst. fr. Etud. andines.* **22**: 1–161, In: *Rech. sur gr. Civ.*, Mém.N°6, Paris: A.D.P.F.
MUIZON, CH. DE. 1981b. Une interprétation fonctionnelle et phylogénétique de l'insertion du psoas major chez les Phocidae. *C. r. hebdo. Séanc. Acad. Sci Paris* **292**: 859–862.
MUIZON, CH. DE 1981c. Le grand voyage des phoques. *La Recherche* **12**: 750–752.
MUIZON, CH. DE. 1982. Dispersion des Monachinae (Phocidae, Mammalia) dans l'hémisphère Sud. *9e Réun. Ann. Sci. Terre. Paris: Soc. Géol. Fr.*: 463.
MUIZON, CH. DE. In press. Les relations phylogénétiques des Lutrinae (Musteloidea, Mammalia). In: Phylogénie et paléobiogéographie. *Géobios Mém. Spéc.* No. 7.
MUIZON, CH. DE & BELLON, H. 1980. L'âge mio-pliocène de la Formation Pisco (Pérou). *C. r. hebdo. Séanc. Acad. Sci. Paris* **290**: 1063–1066.
MUIZON, CH. DE & BOND, M. 1982. Le Phocidae miocène de la Formation Paraná (Entre Ríos, Argentine). *Bull. Mus. natn. Hist. nat. Paris* (4e ser. sect. C) **4** (2) (in press).
MUIZON, CH. DE & HENDEY, Q. B. 1980. Late Tertiary seals of the South Atlantic Ocean. *Ann. S. Afr. Mus.* **82**: 91–128.
NELSON, G. 1974. Classification as an expression of Phylogenetical relations. *Syst. Zool.* **22**: 344–359.
NORDMANN, A. VON. 1860. *Paleontologie Sudrusslands.* IV. *Elephas, Mastodon, Dinotherium, Phoca, Manatus, Cetotherium, Balaena, Balaenoptera* und *Delphinus*: 271–360. Helsingfors: Früs, H. C.
ORLOV, J. A. 1933. *Semantor macrurus* (ordo Pinnipedia, Fam. Semantoridae fam. nova) aus den Neogen Ablagerungen Westsiberiens. *Trudȳ paleozool. Inst.* **2**: 165–262.
PIERARD, J. 1971. Osteology and Myology of the Weddell seal *Leptonychotes weddelli* (Lesson 1826). In: BURT, W. H. ed. *Antarctic Pinnipedia. Antarct. Res. Ser.* **18**: 53–108. Washington: AGU.
PIVETEAU, J. 1961. *Traité de paléontologie. Mammifères, origine reptilienne, évolution* **6** (2): 1–1138. Paris: Masson et Cie.
POMEROL, CH. 1973. *Stratigraphie et Paléobiologie. Ere cénozoique (Tertiaire et Quaternaire)* Paris: Doin.
RAY, C. E. 1976a. *Phoca wymani* and other Tertiary seals (Mammalia: Phocidae) described from the eastern seabord of North America. *Smithson. Contr. Paleobiol.* **28**: 1–36.
RAY, C. E. 1976b. Geography of phocid evolution. *Syst. Zool.* **25**: 391–406.
REPENNING, C. A. 1972. Underwater hearing in seals: functional morphology. In: HARRISON, R. J. ed., *Functional anatomy of marine Mammals* 1: 307–331. London, New York: Academic Press.
REPENNING, C. A. & RAY, C. E. 1977. The origin of the Hawaiian monk seal. *Proc. biol. Soc. Wash.* **89**: 667–688.
REPENNING, C. A., RAY, C. E. & GRIGORESCU, D. 1979. Pinniped biogeography. In: GRAY, J. & BOUCOT, A. J. eds. *Historical biogeography, plate tectonics and the changing environment*: 357–369 Corvallis: Oregon State University Press.
REPENNING, C. A. & TEDFORD, R. H. 1977. Otarioid seals of the Neogene. *Prof. Pap. U.S. geol. Surv.* **992**: 1–93.
ROEP, T. B. & VAN HARTEN, D. 1979. Sedimentological and ostracodological observation on Messinian post-evaporite deposits of some southeastern Spanish Basin. VIIth Intern. Congr. Medit. Neog., Athens 1979. *Annls geol. Pays hell.* (h.s.): 1037–1044.

ROMER, A. S. 1966. *Vertebrate Paleontology.* 3rd ed. Chicago: University Press.

ROUCHY, J. M. 1979. La sédimentation évéporitique messinienne sur les marges méditerranéennes. VIIth Intern. Congr. Medit. Neog., Athens 1979 *Annls geol. Pays hell.* (h.s.) 1051–1060.

SARICH, V. M. 1969a. Pinniped origins and the rate of evolution of carnivore albumins. *Syst. Zool.* **18**: 286–295.

SARICH, V. M. 1969b. Pinniped phylogeny. *Syst. Zool.* **18**: 416–422.

SARICH, V. M. 1975. Pinniped Systematics immunological comparison of their albumins and transferins. *Am. Zool.* **15**: 82.

SARRA, R. 1930. Thiodontoliti ed altri avanzi fossil del Cretaceo e Tertiario rinvenuti in Basilicata *Riv. ital. Paleont. Stratigr. Parmes* **3–4**: 47–52.

SAVAGE, R. J. G. 1957. The anatomy of *Potamotherium*, an Oligocene Lutrine. *Proc. zool. Soc. Lond.* **129**: 151–244.

SCHEFFER, V. B. 1958. *Seals, sea lions and walruses.* Standford: University Press.

SCHMIDT-KITTLER, N. VON. 1981. Zur Stammesgeschichte des marderverwandten Raubtiergruppen (Musteloidea, Carnivora). *Eclog. geol. Helv.* **74**: 753–801.

SCOPOLI, G. A. 1777. *Introductio ad historiam naturalem sistens genera lapidum, plantarum et animalium* **6**: 506 + 34. Praha.

SIMIONESCU, I. 1925. Foci fosile din Sarmatecul de la Chisinau. *Memle Sect. Stiint. Acad. rom* **3**: 179–191.

SIMPSON, G. G. 1945. The principles of classification and a classification of Mammals. *Bull. Am. Mus. nat. Hist.* **85**: 1–350.

SORBINI, L. & TIRAPELLE RANCAN, R. 1979. Messinian fossil Fish of the Mediterranean. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **29**: 143–154.

TAVANI, G. 1942a. Revisione dei resti di Pinnipedi conservato nel Museo di Geologia di Pisa. *Palaeontogr. ital.* **40**: 97–113.

TAVANI, G. 1942b. Revisione dei resti di Pinnipedi conservati nel Museo geo-paleontologico di Firenze. *Memorie Soc. tosc. Sci. nat.* **61**: 34–42.

TAYLOR, W. P. 1914. The problem of aquatic adaptation in the Carnivora, as illustrated in the osteology and evolution of the Sea-Otter. *Univ. Calif. Publs geol. Sci.* **7**: 465–495.

TEDFORD, R. H. 1976. Relationship of Pinnipeds to other Carnivores (Mammalia). *Syst. Zool.* **25**: 363–374.

THENIUS, E. 1949a. Die Lutrinen des steirischen Tertiärs. *Sber. öst. Akad. Wiss.* I **158**: 299–322.

THENIUS, E. 1949b. Über die systematische Stellung der Genera *Promeles* und *Semantor. Sber. öst. Akad. Wiss.* I **158**: 323–338.

THENIUS, E. 1950. Ergebnisse der neuntersuchung von *Miophoca vetusta* Zapfe (Phocidae, Mammalia) aus dem Torton des Wiener Beckens. *Anz. öst. Akad. Wiss. Mathematische-Naturwissenschaftliche Klasse* **5**: 99–107.

THENIUS, E. 1952. Die saugetierfauna aus dem Torton von Neudorf an der March (ČSR). *Neues Jb. Geol. Paläont. Abh.* **96**: 27–136.

THENIUS, E. 1969. Stammesgeschichte der Säugertiere. *Handbuch der Zoologie* **8** (2): 1–772. Berlin: De Gruyter.

THENIUS, E. 1972. *Grunzüge der Verbreitungsgeschichte der Säugertiere.* Stuttgart: Fischer, G.

TOTH, G. 1944. Weitere Reste von *Miophoca vetusta* Zapfe aus dem Torton des Wiener Beckens. *Paleobiologica* **8**: 173–194.

TOULA, F. 1898. *Phoca vindoboniensis* von Nussdorf in Wien. *Beitr. Paläont. Geol. öst. -Ung.* **11**: 47–70.

UGOLINI, R. 1902. Il *Monachus albiventer* Bodd. del Pliocene di Orciano. *Palaeontogr. ital* **8**: 1–20.

VAN DEN BRINK, F. S. & BARRUEL, P. 1971. *Guide des Mammifères sauvages de l'Europe occidentale* Neuchâtel (Suisse): Delachaux & Niestlé.

VAN BENEDEN, P. J. 1859. Ossements fossiles découverts à Saint-Nicolas en 1859. *Bull. Acad. r. Sci. Belg.* **8** (11): 123–146.

VAN BENEDEN, P. J. 1887. Description des Ossements fossiles des environs d'Anvers. *Ann. Mus. r. Hist. nat. Belg.* **1**: 1–88.

VIRET, J. 1955. Les Pinnipèdes fossiles. *In:* GRASSÉ, P. P., *Traité de Zoologie* **17**: 336–340. Paris: Masson.

ZAPFE, H. 1937. Ein Bemerkenswerter Phocidenfund aus dem Torton des Wiener Beckens. *Verh. zool. -bot. Ges. Wien* **86–87**: 271–276.